University of Alberta

Characterization and evaluation of tree, maize, and upland rice genetic resources in the Azuero region of Panama

by

Brian Edward Love

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Abstract

Plant genetic resources provide the foundation for our agricultural systems. Agroforestry systems make particularly intensive use of plant genetic resources because they often integrate trees with food crops. I conducted a number of studies designed to characterize and evaluate some of the important plant genetic resources (staple grain crops and native timber species) of the Azuero region of Panama. Forty-six maize populations and 52 upland rice populations were collected from subsistence farmers and characterized phenotypically. Additionally the maize populations were molecularly characterized using microsatellites. Substantial phenotypic and molecular diversity was documented, and phenotypic variation was associated with farmers' naming practices as well as concepts of "traditional" and "modern" varieties. A field survey was administered to maize and upland rice farmers and I discovered that most of the crop traits (yield, stress, and plant traits) of importance to farmers are being studied by formal plant breeding programs. Initial performance results of a study of four native timber species suggests that on-station trials give higher survival and growth estimates than on-farm trials. Species differed in survival as well as height and basal diameter growth rates, but not in wood volume index growth rates. These same native timber species were evaluated for their performance in a living fence and open-pasture in an actively grazed pasture. The living fence offered protection to establishing seedlings except in cases where tree species were palatable to cattle. Together these studies provide baseline information about existing plant genetic resources as well as insight into how diversity can be established and maintained in agricultural landscapes in Panama.

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TABLE OF CONTENTS

1.0 Panama's history, agriculture, and plant genetic resources: a literature review and thesis outline 1
1.1 Panamanian and Azuero Peninsula biogeographical history and demographics. 1
1.2 Panamanian climate, vegetation, and soils 1
1.3 Agriculture in Panama 2
1.4 Plant genetic diversity in Panama and the world 4
1.5 Literature review conclusions 5
1.6 Development of thesis research 6
1.7 Structure of the thesis 7
1.8 Research objectives and hypotheses 8
2.0 Agrobiodiversity: its value, measurement and conservation in the context of sustainable agriculture 12
2.1 Abstract 12
2.2 Introduction 12
2.2.1 Agrobiodiversity 12
2.2.2 Sustainability 13
2.2.3 In-situ and ex-situ conservation 13
2.2.4 Theoretical underpinnings of conservation 14
2.2.5 Past reviews 15
2.2.6 Historical context 15
2.3 Value of agrobiodiversity 17
2.4 Measurement of agrobiodiversity 20
2.4.1 Landrace defined 20
2.4.2 Quantification of diversity 21
2.4.3 Measures of diversity 22
2.4.4 Genetic diversity parameters 24
2.4.5 Genetic data 25
2.4.6 Sampling approaches 27
2.4.7 Analytical statistics for diversity measures 28
2.4.8 Functional diversity 29
2.5 Comparison of in-situ and ex-situ conservation strategies 31
2.5.1 Advantages of in-situ conservation 31
2.5.2 Disadvantages of in-situ conservation 32
2.5.3 Incentives for in-situ conservation 33
2.5.4 Advantages of ex-situ conservation 35
2.5.5 Disadvantages of ex-situ conservation 36
2.6 Seed exchange 38
2.7 Ethics and farmers' rights 39
2.8 Conclusions 40
3.0 Designing and conducting on-farm surveys of resource-poor farmers' agricultural systems: a practical review 42
3.1 Abstract 42
3.2 Introduction 42
3.3 Preliminary on-farm surveys 44

3.3.1 History 45
3.3.2 Experimental design 45
3.3.3 Sampling techniques 49
3.4 Surveying people: interviews 52
3.4.1 General interview structure 52
3.4.2 Interview questions 53
3.4.3 Interview organization 56
3.4.4 Interview physical and social setting 57
3.5 Pre-testing surveys 60
3.6 Conclusions 60
4.0 Collection and characterization of maize and upland rice populations cropped by subsistence farmers in the uplands of Panama's Azuero region 61
4.1 Abstract 61
4.2 Introduction 61
4.3 Materials and methods 63
4.3.1 Study Site 63
4.3.2 Collection strategy 63
4.3.4 Molecular characterization 66
4.3.5 Statistical analysis 67
4.4 Results and discussion 68
4.5 Conclusions 72
4.6 Tables 73
4.7 Figures 75
5.0 Maize and upland rice traits of importance for farmers practicing manual rainfed agriculture in the humid tropics: a Panamanian case-study 79
5.1 Abstract 79
5.2 Introduction 80
5.3 Methods 81
5.3.1 Study area 81
5.3.2 Farmer selection and interview procedures 82
5.3.3 Analyses procedures 83
5.4 Results 84
5.4.1 Sample characteristics 84
5.4.2 Crop traits 84
5.4.3 Upland rice 85
5.4.4 Maize 86
5.5 Discussion 86
5.5.1 Traits of importance to subsistence farmers 87
5.5.1.1 Rice 87
5.5.1.2 Maize 88
5.5.2 Comparing maize and rice 90
5.5.3 Future considerations for survey methods 90
5.5.4 Crop ideotypes 91
5.6 Conclusions 92
5.7 Figures 94
5.8 Tables 95

6.0 Evaluation of the initial performance of four native timber species under on-farm and on-station trial conditions in Panama **98**
6.1 Abstract **98**
6.2 Introduction **99**
6.3 Materials and methods **100**
6.3.1 Study site 100
6.3.2 On-farm trial design 101
6.3.3 On-station selection trial design 103
6.3.4 Statistical methods 103
6.4 Results **105**
6.5 Discussion **107**
6.6 Conclusions **112**
6.7 Figures **114**
7.0 Tree seedling establishment in living fences: a low-cost agroforestry management practice for the tropics **118**
7.1 Abstract **118**
7.2 Introduction **119**
7.2.1 Tree establishment in pastures 119
7.2.2 Living fences 119
7.3 Materials and methods **121**
7.3.1 Study site 121
7.3.2 Experimental design 122
7.3.3 Field methods: living fence planting 122
7.3.4 Field methods: plantation planting 124
7.3.5 Statistical analysis 125
7.4 Results **126**
7.4.1 Living fence characteristics 126
7.4.2 Seedling survival and acceptability 126
7.4.3 Absolute and relative growth performance 127
7.4.4 Cattle damage 128
7.5 Discussion and conclusions **129**
7.6 Figures **134**
7.7 Tables **140**
8.0 General conclusions and contributions to knowledge **142**
8.1 Research findings **143**
8.1.1 Characterization of maize and upland rice 143
8.1.2 Performance of native timber species 144
8.3 Contributions to knowledge **145**
8.3 Recommendations for future research **147**
8.3.1 Characterization of maize and upland rice diversity 147
8.3.2 Initial performance of native timber species 147
9.0 Literature cited **148**
10.0 Appendices **181**

LIST OF TABLES

Table 4.1 Means and ranges for selected maize and upland rice traits and least-squared means for traits that differed between "modern" and "traditional" populations collected from farmers in Panama, 2005. 73
Table 4.2 The percent of maize and upland rice populations exhibiting presence of selected nominal traits measured in an agromorphological trial in Panama, 2005... 74
Table 5.1 Traits belonging to specific categories reported by at least 10% of farmers (%F) for maize and upland rice populations cropped in 2004 in the humid tropics of Panama. The percent of populations with the positive (%Pos) and negative (%Neg) variants of the trait are given 95
Table 5.2 Maize and upland rice traits that at least 10% of farmers (%F) reported to be desirable in new varieties, Panama, 2004. 96
Table 5.3 Important traits reported by farmers for maize and upland rice based on trait preference and desirability in new varieties Panama, 2004 97
Table 6.1 P-values for fixed factors in mixed model analysis of on-farm, on-station, and combined datasets of four native-timber species grown in Panama at two locations. 115
Table 6.2 Average final basal diameter, height and wood volume index after two years of growth on-station and on-farm in Panama, for each of four native timber species planted at Rio Hato and Los Santos. 116
Table 6.3 Least-squares means and 95% confidence intervals (CI) for average monthly growth increment in basal diameter, height, and wood volume index during the first two years of growth for each of four native timber species planted on-farm and on-station at two locations in Panama. Results are for mixed model analysis conducted separately for on-farm and on-station trial data, as well as for combined data. Treatments followed by different letters differ significantly ($P \leq 0.05$); within a column lowercase letters compare species while uppercase letters compare locations or trial types. 117
Table 7.1 Mean (± 95% confidence interval) characteristics of the nearest living stakes adjacent to planted tree seedlings within living fences..... 140
Table 7.2 Seedling survival and means (± 95% confidence interval) for seedling final height and final basal diameter after 2 years of growth for each of four native tree species established in either a living fence, open-pasture, or a monoculture plantation. Means are least-squared means except for means in the "All species" and "Plantation" categories, which are unadjusted means..... 141

LIST OF FIGURES

Figure 4.1 Flow chart outline of the laboratory proceedure used for genotyping based on bulked maize DNA. 75
Figure 4.2 Cluster dendrogram (Gower's distance, Ward's method, phenotypic and molecular data) of maize populations collected from farmers in Panama, 2005..... 76
Figure 4.3 Cluster dendrogram (Gower's distance, Ward's method, phenotypic data) upland rice populations collected from farmers in Panama, 2005..... 77
Figure 4.4 Ordination (Euclidean distance, Non-metric multi-dimensional scaling, molecular data) of maize populations collected in Panama in 2005 and populations collected elsewhere in Latin America (B = Bolivia (n = 1), C = Cuba (n = 1), E = Ecuador (n = 1), G = Guatemala (n = 1), M= Mexico (n = 4), P = Panama (n = 49), PE = Peru (n = 1)). 78
Figure 5.1 Study site towns in Herrera province, Panama..... 94
Figure 6.1 Map showing forest cover (shaded areas) in Panama in 1992, and the location and rainfall (mm year^{-1}) of the two experimental areas: Los Santos and Rio Hato for on-station and surrounding on-farm trials (ANAM, 1992 map produced from SIG Republic, Eon Systems, all rights reserved). 114
Figure 7.1 Geographical location of the El Cacao experimental site in the Republic of Panama. 134
Figure 7.2 Layout of experimental plots in the living fence field trials in Panama, 2004-2006..... 135
Figure 7.3 Total survival of tree seedlings planted in either living fences or open pasture in Panama, 2004-2006. 136
Figure 7.4 Seedling survival of each of four native tree species planted in either open-pasture or a living fence after 2 years of growth in Panama, 2004-2006. Significant differences between planting positions (open-pasture, living fence) are indicated for each category. 137
Figure 7.5 Proportion of seedlings exhibiting acceptable growth for timber production for each of four native tree species planted in either open-pasture or a living fence after 2 years of growth in Panama, 2004-2006. Significant differences between planting positions (open-pasture, living fence) are indicated for each category. 138
Figure 7.6 Means ± 95% confidence interval for relative height growth of seedlings after 2 years for each of four native tree species planted within either a living fence or open-pasture in Panama, 2004-2006. With the exception of the "All species" category, means are least-squared means. 139

LIST OF APPENDICES

Appendix 3.1 Glossary of technical terms used in on-farm survey based studies..... 181
Appendix 4.1 PCR master mix recipes for the amplification of different microsatellite marker in bulked maize DNA samples. 182
Appendix 4.2 PCR reaction programs for microsatellites amplified in bulk DNA samples of maize populations collected in Panama. 183
Appendix 4.3 The size and average frequency of alleles detected in Panamanian maize populations by different microsatellite markers. 185
Appendix 5.1 Informed consent document used to outline farmers' rights..... 186
Appendix 5.2 Interview format used to obtain data on maize and upland rice traits of importance to subsistence farmers in Panama. 187

1.0 Panama's history, agriculture, and plant genetic resources: a literature review and thesis outline

1.1 Panamanian and Azuero Peninsula biogeographical history and demographics

Panama is a sigmoid-shaped isthmus of 75 500 km^2 that links Colombia to Central America (7° and 9° N and 77° and 83° W). It is thought Panama is geologically one of the newest parts of Central America, with the eastern part of the Panamanian isthmus rising completely out of the sea only three million years ago (Coates, 1997). The Azuero peninsula 7° N and 80° W (Jaen-Suarez, 1978) is an exotic terrain which formed thousands of kilometres away from Panama before being deposited on the isthmus (Coates, 1997). Two provinces, Herrera and Los Santos, largely cover the Auzero peninsula, which is thought to be the first region inhabited by Amerindians and later colonized by the Spanish (Holdridge, 1967). Panama's population stands at 2.9 million (World-Bank, 2002), giving a population density of 38 inhabitants/km^2. Forty-three percent of Panama's population is rural and 37% lives below the poverty line (World-Bank, 2002), with poverty being more pronounced in rural than urban areas (Elton, 1997).

1.2 Panamanian climate, vegetation, and soils

Panama is located in the tropics, which is geographically defined by the tropics of Capricorn (23° 27'00" S) and Cancer (23° 27'00" N). The tropics are characterized by diurnal changes in temperature that are greater than seasonal changes, and day lengths that vary little (Dennett, 1984). Precipitation in Panama ranges from slightly under 1000

to 7000 mm annually (IGNTG, 1988). Near the Caribbean >3000 mm falls annually while near the Pacific <2000 mm falls annually (Condit *et al.* 2002). Annual precipitation in the Azuero Peninsula ranges from 900 to 2100 mm (IRHE, 1998). Annual median temperature in Panama ranges from 14°C, atop the highest mountain, to 27°C along its coasts, while annual median temperatures in the Azuero Peninsula range from 24°C in its mountainous region to 27°C in its lowlands (IGNTG, 1988).

Panama is largely covered by ultisols (FAO-UNESCO, 2005) but regional differences exist. Soils in the Azuero Peninsula include alfisols in the flat dry lands and inceptisols as well as ultisols in the wetter hillier regions (Jaramillo, 1986). Forest is the naturally occurring vegetation of Panama and 12 of Holdridge's forest life zones[3] (IGNTG, 1988) ranging from dry forest to tropical rainforest are present. Forest cover has been reduced from 70% in 1947 to 44% in 1995 (Fischer and Vasseur, 2000). Most of this deforestation has been due to pasture creation with 70% of Panama's deforested land now in cattle pasture (Ledec, 1992). This deforestation process has been most pronounced in the Azuero peninsula, with forest and pasture coverage in Herrera province standing at 4% (ANAM, 1999) and 51% (Contraloría, 2001a), respectively.

1.3 Agriculture in Panama

In 2000, Panama's food imports totalled US $348 million, significantly greater than 1991 when food imports were US $149 million (World-Bank, 2002). In 1991, agriculture accounted for 9% of Panama's Gross Domestic Product (GDP), while in 2000

[3] Holdridge's classification is commonly used in Central and South America. It uses mean annual temperature and precipitation and assumes temperature can be used to estimate potential evapotranspiration. These data are used to define humidity provinces and temperature zones. Each combination of humidity province and temperature zone is a life zone and is characterized by a particular vegetation type (Young 1987).

it made up only 7% of GDP. In contrast, the service sector accounted for 77% of the GDP (World-Bank, 2002). However, GDP does not adequately reflect the importance of agriculture in terms of rural employment, food security, and economic stability in many developing countries (Asian_Productivity_Organization, 1995).

Swidden agriculture began in Panama 7000 years ago (Piperno, 1989) and continues to be a primary production strategy for subsistence farmers in Panama (Fischer and Vasseur, 2000). Swidden agriculture is the practice of clearing and burning small plots which are then cropped for a short period of time and subsequently left to fallow for many years (Greenland, 1975). Subsistence farmers produce crops largely for their own consumption with only tiny surpluses being sold to markets. Often subsistence farmers are labelled "resource-poor". While "poverty" is relative, "resource-poor farmers" have been as farmers whose resources (e.g. capital, land, water) do not permit a secure livelihood (Chambers and Ghildyal, 1985).

Rice (*Oryza sativa* L.) is the most important part of the Panamanian diet, but maize (*Zea mays* L.), manioc (*Manihot esculenta* Crantz), plantain (*Musa* L.), pigeon pea (*Cajanus cajan* (L.) Millsp.) and yams (*Dioscorea* L.) are also subsistence staples (McKay, 1990). Along with annual crops, livestock production is very important in Panama. Panama has approximately 1.5 million head of cattle on 1.5 million ha of pasture (Contraloría, 2001a) and 97% of domestic beef production is consumed within Panama based on 1970-1989 data (BNP, 1990-91). Trees are a common component of agricultural landscapes in Panama (Fischer,,1998). Silvopastoralism (combining trees with pastures) and agrosilvopastoralism (combining trees, pastures, and crops) (Nair,

1993) have become major areas of research interest in Central America (Dagang and Nair, 2003).

1.4 Plant genetic diversity in Panama and the world

Plant genetic diversity refers to the variation in the genetic material of plants and is present as both inter-specific and intra-specific diversity. The conservation and utilization of plant genetic resources have become issues of acute international importance (FAO, 2001a). Of the 120 crop species that are nationally important, three food crops, wheat (*Triticum* L.), rice, and maize provide over half of the food energy that humans consume (FAO, 1998). While the number of crop species is low, most plant genetic diversity exists within crops at the varietal level (Brush, 2004).

Worldwide, plant genetic diversity is being stored in over 1300 germplasm collections that currently hold approximately 1-2 million unique accessions[4] of various plant species (FAO, 1998). Despite these efforts, further collection is thought to be needed to fill gaps for a few major species (e.g. maize) (FAO, 1998). The need for collection and conservation of forest genetic resources (e.g. native tree species) is particularly acute (FAO, 1994). Characterization and evaluation of crop genetic resources is required before they can be utilized (Marshall and Brown, 1975). Characterization of plant genetic diversity can be done by collecting morphological, biochemical, and/or molecular data (Mohammadi and Prasanna, 2003).

Panama has high levels of biodiversity (Polsky, 1992). Tree diversity is particularly pronounced in part because of highly variable climatic conditions (Condit et

[4] An accession is a sample of a crop species taken from a given geographical location at a given time.

al., 2002). Field crop genetic diversity has not been studied very intensively in Panama. Collection missions for maize (Kuleshov, 1930; Lawrence, 1984) and rice (Lawrence, 1984) in the past have been limited and further collection missions have been hampered by lack of funding (CNRFP, 1995). One pedigree study of irrigated rice varieties found Panamanian rice to have a narrow genetic base (Cuevas-Pérez et al., 1992). Currently, information on the genetic diversity of maize and upland rice in Panama is not available in the literature. In contrast, the characterization of tree species diversity is well developed in Panama (Aguilar and Condit, 2001; Condit, 1998; Condit et al., 1993; Condit et al., 2002). However, evaluation of native tree species' performance under plantation conditions is lacking (Condit et al., 1993).

1.5 Literature review conclusions

The collection, conservation, characterization, and evaluation of plant genetic resources are an important international priority. Highly diverse environmental conditions in Panama are associated with high levels of plant genetic diversity. The diverse farming conditions of Panama (e.g. silvopastoralism and agrosilvopastoralism) also promote the cropping of a wide range of plant genetic resources. While this diversity has been well studied for trees, the collection and characterization of field crop genetic diversity has been lacking. Regarding native tree species, there is a lack of evaluation data for performance under plantation conditions. Maize and upland rice are the staple crops of Panama and offer an opportunity to collect and characterize plant genetic resources of potential importance. Evaluation of native timber species performance under plantation conditions is now required to demonstrate the utility of

Panáma's native tree diversity. This, in turn, could lead to the reintroduction of tree diversity into landscapes originally deforested during pasture creation.

1.6 Development of thesis research

In 2004, at the University of Alberta under Dr. Dean Spaner's supervision I completed my M.Sc. studies which examined "Trees in pastures in Herrera province, Panama, with emphasis on small-scale farmers" (Love, 2004). This research allowed me to experience first hand the agricultural systems of Panama. During my field research, I would often come across complex agroforestry systems bursting with species and varietal diversity. At the time I was studying tree species diversity in pastures (Love and Spaner, 2005) and I became interested in the different varieties of maize and upland rice that farmers were cultivating. This led me to develop an interest in plant genetic resources. It became apparent that working with plant genetic resources involved both characterizing genetic diversity as well as evaluating the performance of varieties and species. Having studied the species diversity of trees in pastures, I started to contemplate the potential of different tree species for reforestation of pasture landscapes through plantation forestry. These different experiences drove me to engage in Ph.D. research examining the genetic diversity of maize and upland rice as well as the performance of native tree species under plantation conditions.

Early in the research, I realized crop genetic diversity was partially driven by farmers' preference for different crop traits and that plantation forestry in pasture landscapes was potentially complicated by livestock breaches and farmers' preference to plant trees along field boundaries. I thus broadened the scope of my research to include:

1) the investigation of farmers' preferences for specific crop traits and 2) the evaluation of native timber species in living fences in actively grazed pastures. The Ph.D. research developed as two separate lines of investigation linked by the common theme of agrobiodiversity. The first line of research examined crop genetic diversity being farmed and the crop traits of interest to farmers. This study was largely deseriptive in nature. Through it I sought to establish baseline information about existing maize and upland rice diversity, and to describe the crop traits of interest to farmers. The second line of research evaluated the performance of native timber species in plantations and in the living fence of an actively grazed pasture. This study focused on native timber species because of my interest in practical methods for re-establishing native tree diversity in pasture landscapes and the need for evaluation data on the potential of different species (diversity) for reforestation. Researcher managed trials (on-station trials) were compared to trials established on farms with both farmer and researcher input (on-farm trials) in order to compare performance under optimal conditions with performance under conditions approximating farmer management.

1.7 Structure of the thesis

The thesis research was developed as individual manuscripts suitable for submission as articles to peer-reviewed journals. These manuscripts have been slightly altered from their original form in order to conform to a single format and style. Chapters 2 and 3 review the literature on agrobiodiversity and on-farm survey techniques, respectively. Chapters 4 through 7 constitute the data chapters of the thesis that are based on activities and experiments carried out in Panama from 2004-2007. Specifically,

chapter 4 describes maize and upland rice genetic diversity cropped by subsistence farmers. Chapter 5 examines the agronomic traits of maize and upland rice that are of interest to subsistence farmers. Chapter 6 reports on the initial performance of native timber species under plantation management conditions. Chapter 7 investigates the potential of using living fences as a protective barrier when establishing trees in grazed environments. Finally, chapter 8 provides a summary of findings and articulates how they contribute to scientific knowledge and lead to future research.

1.8 Research objectives and hypotheses

This PhD thesis aimed to: 1) describe aspects of maize and upland rice diversity as cropped by subsistence farmers in the Azuero region of Panama and 2) evaluate the initial performance of native timber species in Panama. Much of the diversity work was descriptive rather than experimental in nature. Hypotheses regarding diversity centered on the structure of genetic diversity and crop traits of importance to farmers. The native timber species work was more experimental in nature and explored traditional hypotheses regarding the effects of experimental factors (e.g. location and species) on performance. Descriptive research on native timber species focused on the practical aspects of executing on-farm agroforestry trials.

The specific objectives and hypotheses of this thesis' data chapters were:

Chapter 3 – Genetic diversity of maize and upland rice

Objectives:

1. To collect and characterize the crop genetic diversity for maize and upland rice, farmed by subsistence farmers in Panama.
2. To provide baseline information on diversity and phenotypes and their relationship to farmers' classifications.

Hypotheses:

1. Genetic relationships will partially agree with naming practices and this will be more pronounced for rice (an inbreeding species) than for maize (an outcrossing species).
2. Phenotype will be associated with concepts of "modern" and "traditional" varieties, and genetic distance will be positively associated with geographical distance.
3. Heterogeneous rice populations will be collected and often heterogeneity will be due to admixture of identifiable varieties.
4. Maize populations collected in Panama today will be molecularly distinct from maize populations collected in the past in other parts of Latin America.

Chapter 4 – Maize and upland rice crop traits of interest to subsistence farmers

Objectives:

1. To implement a simple field survey method for identifying crop traits of importance to subsistence farmers.
2. To empirically assess the importance of maize and upland rice traits.

3. To compare and contrast important traits with formal breeding program objectives.

Hypotheses:

1. A large number of crop traits will be identified but only a subset of these traits will be mentioned frequently.
2. The reasons particular crop traits are of interest will be related to the agronomic practices and cultural preferences of farmers.
3. The crop traits that are important to subsistence farmers will differ from those being studied by breeding programs.

Chapter 5 – Initial performance of native timber species under plantation conditions

Objectives:

1. To assess the initial performance (survival and growth) under plantation management of four native timber species at two locations using both on-station and on-farm trials.
2. To describe some of the practical aspects of on-farm agroforestry trial implementation.

Hypotheses:

1. Species will differ in survival and growth.
2. Locations will differ in survival and growth.

3. On-station trial survival and growth results will be greater than those of the on-farm trial.
4. Growth will be negatively associated with topographic slope.

Chapter 6 – Initial performance of trees established in the living fence of an actively grazed pasture

Objectives:

1. To evaluate the potential of a living fence to serve as a protective barrier during tree establishment in an actively grazed pasture.

Hypotheses:

1. Survival and growth will differ between species.
2. Survival and growth will be greater in the living fence than in open-pasture.
3. Livestock-induced damage (trampling, browsing, rubbing) will be greater in open-pasture than in the living fence.
4. Lower growth and survival will be associated with livestock damage.

2.0 Agrobiodiversity: its value, measurement and conservation in the context of sustainable agriculture[5]

2.1 Abstract

Conservation of agrobiodiversity is an important component of sustainable agriculture and is important internationally. To date, ex-situ conservation in genebanks has been the dominant strategy. Recently, in-situ conservation has been advocated as a complementary strategy. This review 1) defines the context of agrobiodiversity conservation, 2) discusses its value and measurement, 3) explores the advantages and disadvantages of ex-situ and in-situ conservation approaches, and 4) outlines the importance of seed exchange and ethical concerns.

2.2 Introduction

2.2.1 Agrobiodiversity

Biodiversity (biological diversity) is the variability among living organisms and the ecological complexes (e.g. ecosystems) they compose (UNCED, 1992). Agrobiodiversity refers to the diversity of living organisms (e.g. plants, animals, bacteria) used in agriculture (Wood and Lenne, 1999). This review is limited to plant diversity and will focus on food plants. Thus, the terms 'crop genetic resources' and 'agrobiodiversity' will be used interchangeably. Agrobiodiversity underpins the development of sustainable agriculture (Ceccarelli et al., 1992; Cleveland et al., 1994). Globally, there are an estimated 250 000 to 500 000 plant species (FAO, 1998). Of these, only 1 500 have been

[5] This chapter, as developed by B. Love and D. Spaner, has been accepted for publication in the *Journal of Sustainable Agriculture*.

used in agriculture (Wilkes, 1993). Currently, there are 120 nationally important crops, and three food crops, wheat (*Triticum* L.), rice (*Oryza* L.) and maize (*Zea mays* L.), provide over half of the food energy consumed by humans (FAO, 1998). While the number of crop species is low, most agrobiodiversity exists within crops at the varietal level (Brush, 2004). Crop plant relatives are also an important component of agrobiodiversity (Hawkes, 1977).

2.2.2 Sustainability

There is no widely accepted definition of sustainable agriculture (Lewandowski et al., 1999). This review treats sustainable agriculture relative to its ecological conceptualization and defines it as the management and utilization of agroecosystems in a manner that does not degrade resources beyond recuperation, and permits indefinite future use by maintaining biological integrity and functionality. Agrobiodiversity constitutes the biological underpinning of agriculture (Fowler and Hodgkin, 2004). Experiments in natural and microcosm environments have linked biodiversity to increased productivity (Tilman et al., 1996), increased stability (McNaughton, 1977), and increased ecosystem functioning (Naeem et al., 1994). Thus, agrobiodiversity contributes to the sustainability of agricultural systems.

2.2.3 In-situ and ex-situ conservation

Conservation strategies may be either ex-situ or in-situ (Maxted et al., 1997; UNCED, 1992). Ex-situ strategies conserve diversity outside of natural habitats, while in-situ strategies conserve diversity in the setting where it developed (UNCED, 1992).

Ex-situ conservation includes genebank storage (seed and field), in-vitro storage, pollen storage, and DNA storage (Maxted et al., 1997). Seed genebanks are the most common storage practice (FAO, 1998). Generally, ex-situ conservation for plant breeding involves the collection, classification, evaluation and utilization of agrobiodiversity (Marshall and Brown, 1975).

In-situ conservation includes conservation in reserves, on farms, and in home gardens (Maxted et al., 1997). In this review on-farm and homegarden conservation are considered to be the same and referred to as on-farm conservation. Reserve strategies apply to forests and wild crop relatives and will only be considered historically. Iltis (1974) suggested a reserve strategy for food crops in which the genetic landscape would be frozen by isolating it spatially and temporally. However, traditional communities are agriculturally dynamic (Louette, 1999), often rendering such a strategy untenable.

On-farm conservation encourages farmers to continue selection and management of local crop populations (Brush, 1999). On-farm conservation has focused on de facto conservation in centers of origin (Brush, 1991; Qualset et al., 1997), but exceptionally valuable varieties are found outside their centers of origin (Vavilov, 1951). Subsistence farmers in marginal environments often maintain large amounts of agrobiodiversity (Bellon, 1996; Maxted et al., 2002; Wood and Lenne, 1997).

2.2.4 Theoretical underpinnings of conservation

Population biology and genetics provide theoretical frameworks for ex-situ conservation and in-situ conservation in reserves (Brush, 2004). In contrast, the scientific basis for on-farm conservation has not been well developed (Wood and Lenne, 1997;

Maxted et al. 2002), although Louette (1999) has advocated the use of metapopulation theory for understanding on-farm conservation. Brush (2004) recognized the potential of niche theory and metapopulation theory as explanatory frameworks, but warned their development for natural populations undergoing natural selection may reduce their utility for crop populations that undergo both natural and artificial selection.

2.2.5 Past reviews

Review articles have addressed in-situ (Altieri and Merrick, 1987; Brush, 1999; Hammer, 2003; Wood and Lenne, 1997) and ex-situ (Goodman, 1990; Qualset and Shands, 2005; Wright, 1997) conservation, the measurement of biodiversity (Brown, 1978; Glaubitz and Moran, 2000; Marshall and Brown, 1975; Mohammadi and Prasanna, 2003; Peet, 1974), its value (Bellon, 1996; Brush and Meng, 1998; Wilson and Ehrlich, 1991), seed exchange (Almekinders et al., 1994; Louette et al., 1997), ethics (Brush, 1992; Evenson, 1999), and the role of agrobiodiversity in sustainability (Ceccarelli et al., 1992; Cleveland et al., 1994). In part, this review aims to provide an integration of these topics.

2.2.6 Historical context

In ancient times (2500 BC) the Sumerians, Egyptians, and Chinese were all engaged in plant introduction from abroad (Ryerson, 1933). In the modern era, especially during colonial times, crop species continued to be collected, with botanical gardens being the primary repository for collections (Brockway, 1979; Maxted et al., 1997).

Today the agriculture of most countries is based on foreign plant introductions (Fowler and Hodgkin, 2004).

Linneaus (1707-1778) formalized the classification of living organisms with his work *Systema Naturae* (Dickinson, 1967). Mendel (1822-1884) discovered the principles of heredity (Bateson, 1913). Darwin called attention to diversity (variation within and among living organisms) and its link to heredity and selection pressure, and discussed agricultural diversity (Darwin, 1860; Darwin, 1883). De Candolle suggested crop wild types as a proxy for identifying centers of domestication (de Candolle, 1914). Vavilov (1951) thereafter suggested that centers of crop diversity, coupled with the presence of wild types, indicated centers of origin. At the same time, he pioneered large-scale, long-term, international collecting missions in the 1920s and 30s (Pistorius, 1997).

Early discussion of crop genetic resource conservation dates back to 1890 (Zeven, 1998). Harlan and Martini (1936) and Frankel (1954) raised concerns early on about the loss of crop genetic resources. While the Green Revolution has often been cited as eroding genetic resources (Almekinders and de Boef, 1999; Matson et al., 1997; Tilman, 1998) these assertions may be unfounded (Smale, 1997; Wood and Lenne, 1997). Harlan (1975) described the international response to these concerns. Eventually, the International Board of Plant Genetic Resources[6] (IBPGR) was established in 1974, conducting ~500 collection missions in its first decade of existence (Lawrence, 1984). Worldwide, there are currently ~6 million accessions[7] (1-2 million unique accessions due to duplication) in over 1300 germplasm collections (FAO, 1998). Further collection is

[6] The IBPGR eventually became the International Plant Genetic Resources Institute and then Bioversity International.

[7] An accession is a sample of a crop species taken from a given geographical location at a given time.

still needed for minor species and to fill gaps in a few major species (e.g. maize) (FAO, 1998). The Convention on Biological Diversity (UNCED, 1992) and the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO, 2001a) created a formal international legal mandate for agrobiodiversity conservation.

These agreements have highlighted in-situ approaches. Reserve strategies such as forest reserves (FAO, 1998) or reserves for wild crop relatives (Frankel et al., 1995) have traditionally been employed for in-situ conservation (Brown, 1999; Maxted et al., 2002). For instance the Sierra de Manantalán Biosphere Reserve in Mexico was created to protect perennial teosinte (*Zea diploperennis*) and the Garo Hills Sanctuary in India was developed to protect oranges (*Citrus indica*) (Meilleur and Hodgkin, 2004). On-farm conservation requiring farmer participation is now, also, considered an important in-situ strategy (Brush, 1999; Cromwell and van Oosterhout, 2000; Maxted et al., 2002). While the theoretical benefits of this on-farm conservation have been well developed (Brush, 1999; Maxted et al., 1997), there are only a relatively small number of projects worldwide (see Bretting and Duvick, 1997; FAO, 1998; Jarvis et al., 2000). In-situ and ex-situ strategies are deemed complementary (UNCED, 1992; FAO, 1998), but few conservation programs employ both approaches (Maxted et al. 1997).

2.3 Value of agrobiodiversity

Biodiversity may be valued because of ethical obligation, economic benefits, or preservation of essential ecosystem services (Wilson and Ehrlich, 1991). Plant breeders and farmers approach the value of agrobiodiversity from different perspectives.

Germplasm is used by plant breeders to adapt crops to heterogeneous and changing environments (Bellon, 1996). Agrobiodiversity conservation is important due to the need to broaden the genetic base of crop plants (Cooper et al., 2001), to prevent the loss of uniquely adapted ecotypes (Vavilov, 1957), and to develop crops for local adaptation (Ceccarelli, 1996). The Irish potato famine (Brush, 2004) and the Southern leaf blight of maize epidemic (Harlan, 1972) are examples of the hazards of a narrow genetic base. The Green Revolution of the 1960s produced high yielding crop varieties and increased recognition of the value of crop genetic resources (Brush, 2004; Pistorius, 1997).

Pardey et al. (1998) proposed that agrobiodiversity has three types of value: 1) use value, 2) option value, and 3) existence value. Use value is associated with genetic resources' current effect on yield. Option value is associated with a future unknown use (e.g. resistance to new disease). Existence value is associated with the satisfaction people derive from simply knowing that diversity exists (Bellon, 1996). Agrobiodiversity conservation is a prerequisite for developing sustainable agriculture because it enables plant breeders to address changing environments (e.g. climate change).

The monetary value of modern plant varieties is difficult to estimate and includes the value of agrobiodiversity, plant breeders' work, and other research inputs (FAO, 1998). Annual global markets for products (including agricultural products) derived from genetic resources are estimated to be worth US $500 - $800 billion (ten Kate and Laird, 2000). The incorporation of genes from a rice landrace into an improved rice variety has been estimated to be worth US $50 million (Evenson and Gollin, 1997).

Farmers may plant varieties to prevent their loss (Bellon, 1996), but generally conservation of agrobiodiversity for its own sake is not a farmer objective (Meng et al.,

1998a). Still, de facto conservation by farmers is commonplace (Brush, 1991). Farmers use intraspecific (varietal) diversity to cope with uncertain and heterogeneous farming conditions (Bellon, 1996). Just and Zilberman (1983) theoretically demonstrated planting multiple varieties minimizes risk while maximizing mean economic returns. Yield stability is arguably a benefit of varietal diversity (Ceccarelli et al., 1992; Cleveland et al., 1994). Reviews of the performance of mixtures (Marshall and Brown, 1973; Trenbath, 1974) have found that while mixtures frequently outperform their average component, seldom do they outperform their best component. However, the best component may vary from year to year, making mixtures more stable across time. Greater stability (Cleveland et al., 1994) and the flexibility to address heterogeneous and marginal farming conditions (Bellon, 1996) are direct contributions of agrobiodiversity to sustainability.

Diversity in varietal maturity assists in the scheduling of labor inputs (Zimmerer, 1991). Varietal diversity may be important due to ritual (specific varieties for religious ceremonies) and prestige (varieties valued for their novelty) (Brush, 2004). Both interspecific (crop species) (Fleuret and Fleuret, 1980) and intraspecific (Bellon, 1996) diversity are important for dietary diversification. Bellon (1996) developed a framework for assessing the dynamics of farmer retention of intraspecific diversity. In this framework, farmers are considered to address their farming concerns (e.g. soil types, diet) by choosing varieties that best address each concern (Bellon, 1996). More information is needed to understand if retaining intraspecific diversity is due to a lack of appropriate improved varieties or because it meets special farmer requirements (Brown, 1999).

2.4 Measurement of agrobiodiversity

Diversity can be measured in physically classified units (e.g. species, races, varieties), or in terms of genes. Genetic diversity exists between and within a number of different levels. This review employs definitions adapted from Cleveland et al. (1999):

Species: Is a number of populations, which have the potential to interbreed. In many cases species are able to breed with closely related species (Ellstrand, 2001) making this classification somewhat subjective.

Race: Is a group of related varieties that share a suite of traits that define that race.

Variety: Is a distinct subunit of a crop species. Farmer varieties are subunits of crop species distinct enough to be named by farmers and include both local and exotic materials of improved and unimproved nature.

Population: A group of individual plants of a particular variety managed under the same regime (e.g. farmer X's yellow maize). A seedlot (Louette, 1999) is the portion of the population used in any given year to regenerate the population through planting.

2.4.1 Landrace defined

Landrace is a popular term in crop genetic resources literature. Despite its initial use in 1890, few authors' have attempted to define it (Zeven, 1998). Landraces are thought to be: 1) adapted to local conditions (Brush, 1999; Cleveland et al., 1994; FAO, 1998); 2) highly diverse (Brown, 1999; Brush, 1999; Cleveland et al., 1994; FAO, 1998; Qualset et al., 1997); 3) tolerant of abiotic and biotic stress (Qualset et al., 1997; Zeven,

1998); and 4) the product of farmer selection (Cleveland et al., 1994; FAO, 1998; Swanson and Goeschl, 2000; Vavilov, 1957).

Wood and Lenne (1997) question whether landraces are locally adapted and argue that local adaptation is unlikely unless farmers select for it or farming is carried out in stress-prone environments. Louette (1999) questions the landrace definition by demonstrating seed exchange and cross-pollination make the notion of "local varieties" difficult to define. Regardless, the distinction between the products of formal breeding programs and those arising in agricultural ecosystems is an important one. The term farmer variety as defined above shall be used in this review when discussing agrobiodiversity and includes landraces (populations improved by generations of farmer management and selection), past and current modern varieties (populations improved by formal breeding programs), and creolized varieties (populations resulting from crosses between landraces and modern varieties while under farmer management).

2.4.2 Quantification of diversity

Community ecology has focused on diversity at the species level (Hanski and Simberloff, 1997). Some agrobiodiversity projects have chosen to quantify diversity at the species level (e.g. Zarin et al. 1999), but most agrobiodiversity work is aimed at diversity at the varietal level (e.g. Bellon, 1996; Brush, 2004; Cleveland et al., 1994; Salick et al., 1997). Crop breeding's foundation on genetic principles makes the genetic diversity contained within populations of varieties important (Charcosset and Moreau, 2004). Techniques for quantifying diversity at the species level are well developed, and are applicable/amenable to quantifying diversity at the varietal level. Quantification of

genetic diversity is a rapidly evolving field and involves more complicated measures and techniques.

Knowledge about the diversity contained in crop species and their varieties assists breeders in crop improvement (Mohammadi and Prasanna, 2003). Agrobiodiversity assessment requires estimates of the geographic area farmers' crop species and varieties cover, population size, and inherent genetic diversity (Brown, 1999). Such assessment is needed to develop both ex-situ (Marshall and Brown, 1975) and in-situ (Brown, 1999) conservation strategies.

2.4.3 Measures of diversity

Species/varietal diversity can be measured in a number of different ways. In ecology, species diversity in communities is the object of measurement (Whittaker, 1965). Communities consist of many coexisting populations, and community boundaries can be difficult to define. In agriculture, crop communities are defined by the boundaries of a farmer's field, making community identification less subjective. Community censuses are difficult and samples in the form of quadrats may be taken instead (Whittaker, 1965).

Species richness, total number of species/varieties in a defined space at a point in time (Hubbell, 2001), is the simplest measure of diversity. In agriculture, this would be the total number of crop species sampled within a farmer's field. Species evenness, how many individuals belong to each species in a community, is also a component of diversity (Margalef, 1958). Abundance-diversity curves graphically portray diversity as both richness and evenness (Zarin et al., 1999). Relative species abundance measures how

rare or common species/varieties are (Hubbell, 2001). Unfortunately, it can be difficult to identify individuals in plant communities (Whittaker, 1965) and high planting densities can make counting of individuals inefficient. Percent cover is an alternative measure which is rapid, repeatable, and methodologically robust (McCune and Grace, 2002).

Indices such as the Shannon-Wiener's or Simpson's index combine richness and evenness values to produce a numerical output (McCune and Grace, 2002). There are a multitude of indices for measuring diversity (Peet, 1974). Hurlbert (1971) suggests such indices are meaningless because they have been defined in so many different ways, and he demonstrates there is non-concordance between indices. While species richness does not include a measure of evenness, it is simple and easy to communicate (Purvis and Hector, 2000). The above measures of species diversity can be applied to other taxonomic units, such as crop races or varieties.

Diversity measures are spatially (sample unit) and temporally specific. Three levels of diversity have been recognized: alpha, beta, and gamma (Whittaker, 1965). Alpha diversity is an estimate of the average diversity contained within a sampling unit (community, quadrat) for which diversity is being measured (e.g. crop species, varieties). Beta diversity is a measure of compositional change between sample units (e.g. number of crop species or varieties that change from farmer to farmer). Gamma diversity is a measure of the diversity contained in a number of units belonging to a larger unit (e.g. total number of crop species or varieties grown in an agroecological zone). Alpha and gamma diversity employ the measures (richness, indices) outlined above. Measurement of beta diversity requires different techniques (McCune and Grace, 2002). Condit et al. (2002) used reduction in species similarity across increasing distance as a measure of

beta diversity. Vellend (2001) has discussed the measurement of beta diversity in terms of species turnover along environmental gradients.

Alpha, Beta, and Gamma capture diversity within spatially based sampling units. While spatial diversity is the most common conceptualization of diversity, turnover of species/varieties in time (temporal diversity) is important and can substitute for lack of spatial diversity (Meng et al., 1998b). Brennan and Byerlee (1991) provided a measure for the rate of varietal replacement, which calculates the average age of varieties since release, weighted by the area they cover.

2.4.4 Genetic diversity parameters

A number of different genetic parameters can be used to describe genetic diversity. Hamrick and Godt (1996) used percent polymorphic loci, mean number of alleles per polymorphic locus and Hardy-Weinberg expected heterozygosity averaged across all loci. Proportion of total diversity among populations is also a commonly used genetic parameter (Yang and Yeh, 1992). Wright (1951) developed a number of measures called F-statistics to quantify genetic differentiation between and within populations (Mohammadi and Prasanna, 2003).

There are three F-statistics (F_{IT}, F_{ST}, and F_{IS}), which are types of inbreeding coefficients and measure inbreeding in individuals relative to the total population (F_{IT}), inbreeding in subpopulations relative to the total population (F_{ST}), and inbreeding in individuals relative to their subpopulations (F_{IS}), respectively (Hartl and Clark, 1989). Computation of these parameters is complex, especially if there are unequal sample and

population sizes and there is disagreement regarding the computation and interpretation of these parameters (Weir and Cockerham, 1984).

Nei's G_{ST} is an alternative for F_{ST}, because, in the case of multiple alleles, the definition of F_{ST} only holds true for the special case of random differentiation without selection (Nei, 1973). Both G_{ST} (e.g. Hamrick and Godt, 1997) and F_{ST} (e.g. Pressoir and Berthaud, 2004a) have been used for studying crop genetic diversity. While these measures normally employ molecular data, if additive allelic effects are assumed, an F_{ST} measure for quantitative morphological traits can be derived using variance components (Pressoir and Berthaud, 2004a).

Alternatively, diversity may be usefully measured as genetic distance-similarity. Mohammadi and Prasanna (2003) discuss commonly used measures of genetic similarity based on molecular marker data (Nei and Li's coefficient, Jaccard's coefficient, simple matching coefficient, and modified Roger's distance) and report modified Roger's distance is preferred due to its superior statistical and genetic properties.

2.4.5 Genetic data

The above parameters require data at the genetic level. Techniques for obtaining such data include morphological data, biochemical data, and molecular (genome-based) data (Mohammadi and Prasanna, 2003). Pedigree data may be used as well, but require the assumption that parents of unknown parentage are genetically distinct (Witcombe, 1999).

Measuring morphological traits is the classical method but is indirect because trait expression has both genetic and environmental components (Newbury and Ford-Lloyd,

1997). Studies have used replicated agronomic trials to gather morphological data (e.g. Louette et al., 1997; Patra and Dhua, 1998), but it is also possible to use on-farm measurements for traits that are minimally influenced by the environment (e.g. Salick et al., 1997).

Biochemical markers and molecular markers have become popular for estimating diversity because they are relatively unaffected by the environment. Biochemical markers include the use of protein markers such as isozymes (Brown, 1978) (different forms of an enzyme coded for by a single locus) or chemicals such as terpenes (Glaubitz and Moran, 2000). Biochemical markers have now been superceded by techniques that sample DNA directly (Newbury and Ford-Lloyd, 1997). Several types of DNA-based markers are available including: restriction fragment length polymorphisms (RFLPs), simple sequence repeats (SSRs), random amplified polymorphic DNA (RAPDs), amplification fragment length polymorphisms (AFLPs), and single nucleotide polymorphisms (SNPs). Glaubitz and Moran (2000) review many of these techniques and their properties.

A number of studies have compared the use of different marker systems. In maize populations RFLPs were found to detect more alleles per locus on average than isozymes, although estimates of population differentiation based on these data were similar (Dubreuil and Charcosset, 1998). Pejic et al. (1998) conducted a comparative study of the use of RFLPs, RAPDs, SSRs, and AFLPs in maize inbred lines. They found dendrograms of genetic similarity were comparable for all techniques except RAPDs. SSRs provided the most information about heterozygosity and allele number and AFLPs the least, however, AFLPs were most efficient because they reveal several bands with a

single assay (Pejic et al., 1998). High-throughput methods involving bulking of individuals have been used for SSRs to increase their efficiency (Warburton et al., 2001). The procedural components of these molecular techniques are constantly being improved. Some examples include the development of fast extraction techniques for DNA (Csaikl et al., 1998), high throughput procedures for developing microsatellite (SSR) libraries (Connell et al., 1998), and cooler conductive media for rapid DNA electrophoresis (Brody and Kern, 2004).

2.4.6 Sampling approaches

Acquiring data requires sampling crop plants in the field. Zarin et al. (1999) outlined a methodology for sampling species/varietal diversity using quadrats in farmers' fields and emphasized sampling field borders because they tend to be especially diverse. When using quadrats for sampling a given amount of area many small quadrats will accurately estimate abundance for common species, but often result in an incomplete species list. Conversely, a few large quadrats covering the same amount of area result in more complete species lists, but tend to overestimate the abundance of rare species and give imprecise abundance estimates for common species (McCune and Lesica, 1992). Agricultural systems are human managed and subject recall may be an alternative method for capturing information (Ashby, 1990). Asking farmers what crop species they planted, amount of seed sown, and spacing can provide information on species/varietal richness and evenness without requiring time-consuming and laborious quadrat sampling.

Sampling genetic diversity in the face of high population-to-population differentiation increases the value of prior empirical data (Hamrick and Godt, 1997).

Marshall and Brown (1975) mathematically developed sampling strategies for ex-situ collection missions based on the conservation of all alleles occurring at greater than 5% frequency within a population, being captured 95% of the time. Their calculations led to the conclusion that no more than 50 individual plants should be collected per population, and as many populations (represented by sites) as possible should be sampled (Marshall and Brown, 1975). This approach has the aim of capturing diverse alleles of use in plant breeding. If the aim is to assess diversity, fewer samples are needed. CIMMYT evaluated maize diversity with SSRs using two bulks of 15 individuals (Warburton et al., 2001). Thus, diversity estimates require the collection of fewer individuals.

Mating systems (self-pollinating, cross-pollinating) affect genetic diversity of crop species, with cross-pollinating species generally being more diverse within than between populations (Hamrick and Godt, 1997). However, in the case where self-pollinating crop populations are made up of a number of distinct lines, diversity may also be greater within than between populations (Bekele, 1983; Brush, 2004). Such observations inform sampling strategies as to at what level sampling should be most intensive. Diversity estimates are expensive and often planning is based on proxy measures (e.g. environmental diversity) (Marshall and Brown, 1975).

2.4.7 Analytical statistics for diversity measures

After data have been collected and parameters calculated, analytical statistical techniques can be used to compare diversity. Richness measures can be compared using standard statistical tests such as t-tests, analysis of variance, and generalized linear models among others. Comparison of diversity indices is slightly more complex because

the distributional properties of the index must be known before making comparisons (Hutcheson, 1970). Genetic parameters can be compared in the same way as species richness using standard analytical statistical tests (Hamrick and Godt, 1997).

Multivariate statistics, including clustering and ordination, are used to describe both species diversity and genetic diversity. McCune and Grace (2002) reviewed and provided a practical guide to the use of multivariate statistical techniques for analyzing species diversity. Mohammadi and Prasanna (2003) provide a broad, well-referenced review of these techniques for analyzing genetic diversity. Labate (2000) has described some of the software packages available for analyzing diversity at the genetic level.

2.4.8 Functional diversity

Not all diversity is of equal utility to plant breeders and farmers. Functional diversity is the portion of diversity that is of use to farmers or breeders. The level (alpha, beta, gamma) at which functional diversity is best measured is debatable and likely context-dependent. Alpha diversity provides a good estimate of how many varieties farmers use at the farm level. Beta diversity may be an appropriate diversity measure where farmers use locally adapted varieties or where seed exchange results in rapid varietal turnover. In a situation where a few individuals are responsible for maintaining and redistributing diversity, as is the case of Amuesha shamans maintaining cassava diversity (Salick et al., 1997), gamma diversity may be a pertinent measure of overall available diversity.

Genetic diversity is functional in terms of the traits it controls. The neutral theory of molecular evolution proposed by Kimura (1968) hypothesizes that most genetic

polymorphisms (different alleles) have no adaptive significance. This suggests most nucleotide substitutions in a gene are functionally equivalent (Clegg, 1997). Thus, high levels of diversity at the molecular level may not be a good indication of functional diversity. In maize, morphological traits show much more differentiation between populations than molecular markers, because of divergent selection for functional morphological traits by farmers, despite considerable gene flow among populations (Pressoir and Berthaud, 2004a). Thus, morphological traits of biological importance to farmers may be a superior measure of functional diversity than molecular markers.

The functionality of some traits may not be recognized unless appropriately challenged, as in the case of disease resistance. Basing collection of diversity on only recognizable morphological traits could miss dormant functional diversity. Molecular marker techniques could be linked more directly to functional diversity by selecting markers that are known to lie near or within genes controlling specific traits of interest. Functional groups can be derived from a matrix of traits of interest (Pillar, 1999). Conservation strategies could then be focused on ensuring the conservation of functional groups. Unfortunately, functional groups will shift as traits of interest change or as populations are added to the matrix of traits of interest.

Marshall and Brown (1975) divided alleles into four types based on being rare or common and on being local or widespread. They argued that only local common alleles are worth collecting because widespread alleles will be captured as a consequence of collection and rare alleles are usually deleterious and not worth collecting (Marshall and Brown, 1975). Charcosset and Moreau (2004) suggested conservation of functional diversity could be guided by using molecular markers to reveal alleles currently not

available in elite germplasm and thus worth conserving. Focusing conservation on functional diversity, a constantly changing concept, will involve subjective classification of what is considered functional.

2.5 Comparison of in-situ and ex-situ conservation strategies

2.5.1 Advantages of in-situ conservation

Preservation of evolutionary processes (mutation, migration, recombination, selection) is often cited as a major advantage of in-situ conservation (Brown, 1999). These processes supposedly lead to the evolution of locally adapted crop varieties (Bellon et al., 1997), but empirical evidence is lacking (Wood and Lenne, 1997). Local adaptation in composite crosses has been observed to develop after 12 generations even without human selection (Suneson, 1956). Composite crosses may not be a good model for farmer varieties because compared to farmer managed plant populations, they have a much broader genetic base and survivorship is simpler without selection pressure for non-environmental factors, such as quality, flavor, and size. (Brown, 1999). Zeven (1996) reported rapid and substantial changes occurred in a wheat landrace grown outside of its native region in the 1920s. In-situ conservation can be a backup to ex-situ collections in case of loss (Brush, 1999). Brush (1991) suggested in-situ conservation may be less expensive than ex-situ conservation, however this is not necessarily the case (Smale et al., 2003).

2.5.2 Disadvantages of in-situ conservation

On-farm conservation of landraces by farmers, schools, and agricultural societies was advocated in Europe in 1927, but these activities were unsuccessful due to World War II, lack of funding, and variable teacher enthusiasm (Zeven, 1996). On-farm conservation was again contemplated, but dismissed during the conservation efforts of the 1970s and 80s. This was because plant breeders wanted the conserved materials to be directly available to them and it was also assumed that: 1) agricultural development would inevitably replace existing varieties with modern ones, and 2) monetary compensation would be a necessary incentive for on-farm conservation (Brush, 1999). It has also been assumed farmers cannot be trusted to protect important resources and protecting these resources would condemn conservationist farmers to perpetual poverty (Brush, 1991).

One constant criticism of in-situ conservation is that while it has been advocated, no concrete framework has been developed for its implementation (Brush, 1991; Meng et al., 1998a). More recently, Maxted et al. (2002) and Bretting and Duvick (1997) outlined broad methodologies for on-farm conservation projects. Projects must be flexible enough to adapt to specific circumstances (Maxted et al., 2002) and this hinders the development of general frameworks. In-situ projects have been initiated to test the implementation of in-situ conservation and many of these projects have encountered logistical problems when working with governments and farmers (Jarvis et al., 2000).

The perceived disadvantages may be overcome by a number of initiatives that make conservation of agrobiodiversity more attractive through incentives. Bellon (2004) and Brush (1999) outlined incentives and interventions for facilitating on-farm

conservation. Interventions have been divided into market and non-market interventions (Brush, 1999) and/or supply and demand interventions (Bellon, 2004).

2.5.3 Incentives for in-situ conservation

Direct monetary incentives have been considered and implemented in developed countries such as those of the European Union (FAO, 1998) and developing countries such as Nepal, but it is unknown how long such subsidies can last (Bretting and Duvick, 1997).

Development of markets for the products of farmers' varieties is a market or demand intervention. Niche markets where farmers' varieties are in demand can be identified and constraints to market development (storage, transportation, information, marketing incongruencies) can be alleviated (Brush, 1999). Meng et al. (1998a) found the amount of a traditional variety being marketed was a strong predictor of its conservation. Developing a market that previously did not exist is also possible, as demonstrated by the case of Cherokee maize landraces sold as Indian maize flour (Brush, 1999). This case accessed the large lucrative US market, an unlikely situation for crops in developing countries facing substantial market barriers (Humpal and Guenette, 2000). Brush (2004) suggests development of markets along the line of specialty products (e.g. European appellation marketing) would require an investment larger than the value of the crop diversity it would conserve.

The direct sale of genetic resources is also a potential market. Markets and institutions have been developed to facilitate the sale of genetic resources to the pharmaceutical industry (de Carvalho, 2003). While it is possible to imagine similar

systems for agrobiodiversity, large public collections and the propensity for breeders to work with their own materials makes development of such a market unlikely (Brush, 1999). The University of California at Davis attempted to compensate developing countries for crop germplasm, however, lack of clear ownership makes it difficult to compensate individuals (Ronald, 1998).

Participatory crop improvement is often proposed as an incentive for farmers to conserve crop diversity on farms (Bellon, 2004; Brush, 1999; Maxted et al., 2002; Smale et al., 2003) and is a non-market or supply intervention. Two methods of participatory crop improvement have been outlined: 1) participatory varietal selection (farmer evaluation of finished varieties) and 2) participatory breeding (farmer selection within highly variable populations) (Morris and Bellon, 2004). Brush (2004) asserts participatory varietal selection can reduce on-farm diversity by replacing traditional varieties and suggests emphasis should be on participatory breeding. Regardless of the participatory crop improvement approach used, if use of locally adapted populations is encouraged, so will diversity (Morris and Bellon, 2004).

Evidence from participatory rice variety development in Nepal suggests the products of participatory breeding can be widely adopted (Joshi et al., 2001). This study noted competition between released and traditional varieties, but did not monitor changes in diversity. Participatory breeding should aim to improve farmers' livelihoods by providing access to appropriate agricultural technology (i.e. acceptable varieties). Whether this leads to increased diversity will be case-dependent.

Farmers constantly experiment with new agricultural technologies (Bellon, 2001; Johnson, 1972; Lightfoot, 1984; Lightfoot, 1987; Richards, 1989). Farmer

experimentation with varieties is expressed in high rates of varietal turnover (Bellon et al., 1997). Increasing access to varietal diversity provides farmers with more options for maintaining diversity during varietal turnover. The costs (time, effort, resources) of obtaining seed may be high (Bellon, 2004). Creation of an information-rich environment in which farmers can obtain seed (e.g. CIMMYT's maize landrace project in Oaxaca, Mexico (Smale et al., 2003)), can facilitate the spread and use of crop genetic resources.

Seed exchange may also occur spontaneously at diversity fairs in which farmers gather at central locations to display the crops and varieties they grow (Brush, 1999). Community seedbanks have been established to facilitate access to varietal diversity (Asfaw, 1999; Cromwell and van Oosterhout, 2000). Seed regulatory frameworks often require stringent levels of uniformity and quality that prevent development of heterogeneous materials (high diversity) and restrict farmer participation (Louwaars, 2001; Wolff, 2004). Reform of these laws could improve access. Education campaigns and publicity supporting the conservation of crop genetic resources have also been used to promote conservation (Bretting and Duvick, 1997).

2.5.4 Advantages of ex-situ conservation

The principal advantage of genebanks is that their materials are readily available to plant breeders. Characterization and evaluation of materials and storage of this information in databases also facilitate the process of plant breeding. These collections address the uncertainty of what will be required in the future because they contain a broad range of materials (Smale and Day-Rubenstein, 2002). Storage in genebanks guards against the loss of diversity in agroecosystems (Zeven, 1996) and can facilitate

reintroduction in the case of loss (FAO, 1998). Reintroduction has become especially important in cases of disaster relief following war or natural disasters (Wye-University, 2005). Ex-situ conservation also has the advantage of an established theoretical basis that can guide decision-making regarding the collection, characterization, and utilization of agrobiodiversity.

2.5.5 Disadvantages of ex-situ conservation

Limited use of ex-situ collections by breeders has resulted in the questioning of genebanks' value (Wright, 1997). Plant breeders often prefer to work within their own materials because they can still achieve genetic gains (Cooper et al., 2001) and crossing elite to unimproved materials can degrade the genetic gains of elite breeding lines (Cuevas-Pérez et al., 1992). In contrast, Smale and Day-Rubenstein (2002) have shown germplasm requests from US genebanks are substantial and developing countries are major recipients of distributed materials. It has also been demonstrated the current and future benefits from stored germplasm likely outweigh the costs of ex-situ conservation (Pardey et al., 1998).

Ex-situ conservation has been criticized as being static (Bellon et al., 1997; Brush, 1991). Brush (1991) argues that if diversity is adequately collected today it will quickly become obsolete due to evolution in agroecosystems. This is an extreme view because if a complete collection were obtained formal breeding and introduction programs could mimic these in-situ processes (e.g. crossing, migration, and selection). Even mutation can be induced (van Harten, 1998). However, these programs may not be as cost-effective at carrying out these processes as in-situ conservation.

Collection missions of the IBPGR were thought to have preserved most of the crop plant diversity available at the time (Plucknett et al., 1987). However, poor sampling techniques (Frankel et al., 1995), incomplete data regarding agroecological setting (Bretting and Duvick, 1997), and the focus on a few major species (Lawrence, 1984) were associated with this effort. Only as much as 50% of the genetic variation for minor crops has been sampled and passport data are unavailable for 50% of all accessions (Wright, 1997).

Maintenance of collections is problematic. Regeneration of accessions is costly and funding is often lacking. Regeneration backlogs existed in 66% of developing countries from 1995 to 2000 (Qualset and Shands, 2005). Worldwide only 18% of countries have been able to reduce their regeneration backlogs (Wye-University, 2005). This has resulted in genebanks being referred to as seed morgues (Goodman, 1990). Even if regeneration occurs, random genetic drift is a concern in small populations and can affect allele frequency through loss of heterozygosity and due to the fixation or loss of alleles (Yeh, 2000). Techniques such as those described by Gale and Lawrence (1984) minimize these risks. These techniques do not address the problem of initial samples being inadequately small. Often, farmers may not be able to provide seed from a theoretically optimal number of individuals during collections (Mazzani and Segovia, 1998).

While the advantages seem few and the disadvantages seem many, ex-situ conservation has been the mainstay of agrobiodiversity conservation. This is because it guarantees the conservation of plant genetic resources and makes them available to breeding programs. Core collections are reduced collections that contain most of the

diversity present in all accessions. They can be established on the basis of phenotypic or genetic variability present in all accessions and are less costly to maintain because they consist of fewer accessions (Scippa et al., 2001). Statistical techniques for the selection of core subsets have been developed (Franco et al., 2005; Franco et al., 2006). Screening materials for traits of interest is costly. Optimum search strategies have been outlined to facilitate the use of germplasm when variability that does not exist within breeding lines is needed (Smale, 1998). Such strategies may improve the efficiency of ex-situ conservation.

2.6 Seed exchange

Eighty percent of all seed in developing countries is produced on-farm and seed exchange is one of the ways that local gene pools are maintained (Almekinders and de Boef, 1999). Farming systems are dynamic and involve substantial amounts of seed exchange both within and between communities (Louette et al., 1997). Seed exchange can occur across long distances (Brush et al., 1981). Even small amounts of seed exchange can prevent genetic differentiation in open-pollinated crops (Pressoir and Berthaud, 2004b). Still, adoption of seed declines as distance from source increases (Witcombe et al., 1999), in part because of reduced seed exchange. Local seed exchange is limited in its ability to acquire exotic materials (Almekinders and de Boef, 1999). Exotic materials can increase diversity by being incorporated into a farmer's suite of varieties (Brush, 2004) or through creolization (repeated crossing of modern variety to farmer varieties) in the case of open-pollinated crops (Bellon and Risopoulos, 2001).

Seed exchange networks can facilitate recovery of lost varieties and a network of farmers can maintain many varieties at a lower cost than can an individual farmer (Bellon, 2004). Seed networks can be weak with regards to incentives, information, and resources (Tripp, 2001), but can also be complex, dynamic and efficient (Cromwell, 1990). Certain farmers maintain larger amounts of diversity than others (Meng et al., 1998a). Facilitating seed exchange between these farmers and other farmers can enhance diversity (Cromwell and van Oosterhout, 2000). Farmer seed exchange tends to be based on family ties and traditional social networks (Almekinders et al., 1994). Thus, social barriers tend to prevent seed exchange (Zeven, 1999). Seboka and Deressa (2000) argue government extension programs should become involved in informal seed exchange networks in order to validate them. Seed exchange is ubiquitous and is an important mechanism underpinning defacto in-situ conservation.

2.7 Ethics and farmers' rights

Intellectual property rights (IPRs) have become legally entrenched through the World Trade Organization (WTO), which obligates members to accept its agreement on trade-related aspects of intellectual property rights (TRIPs) and as such plant variety protection through patenting (Alker and Heidhues, 2002). Brush (2004) traces the history of how genetic resource status changed from that of common heritage to that of private property. Breeders' rights have been developing since the 1920s but were limited by breeders' exemption (right to use varieties in breeding) and farmers' privilege (right to save and re-use seed) clauses, until 1991 when these clauses were cut back (Wolff, 2004). Plant variety protection legally prohibits over-the-fence exchange (i.e. from one farmer to

another) of seed (Alker and Heidhues, 2002). However, it is unclear if this is enforceable where informal seed networks is concerned. This is because many users conducting relatively small transactions will likely not merit enforcement. Moreover, developing countries have weak institutions for protecting such rights (Evenson, 1999).

A more realistic concern is that patented products originating from local genetic resources and knowledge will not benefit local people, a phenomenon which has been termed biopiracy (Shiva, 1997). Farmers' rights have been viewed as a response to breeders' rights which permit proprietary claims to finished varieties (Brush, 1992). Farmers' rights have also been proposed as a means by which farmers in poor countries could be compensated for their contribution to the development and maintenance of crop genetic resources (Esquinas-Alcázar, 1998). The ethical issues surrounding the use of plant genetic resources and adequate compensation of those involved in their maintenance will continue to be an important issue in crop genetic resources conservation.

2.8 Conclusions

Agrobiodiversity has become an international priority and is institutionalized through binding international legal agreements. The value of agrobiodiversity is unquestionable, but will also depend on the clientele (e.g. breeders, subsistence farmers). The measurement of agrobiodiversity is a necessary prerequisite for developing conservation strategies. Measurement can be carried out using a number of different methods for a number of different units of analysis (species, varieties, genes). Use of specific methods, units of analysis, and sampling strategies will depend on the objectives

of the conservation program. Likewise, the statistical techniques available for analysis of agrobiodiversity data are numerous and appropriate utilization is dependent on objectives. Implementation of conservation strategies falls broadly into in-situ and ex-situ approaches. While these approaches are deemed to be theoretically complementary, there are few examples of projects implementing integrated approaches. Each of these strategies has advantages and disadvantages, although some are currently debated. Despite these difficulties, it is clear that the conservation of agrobiodiversity is a prerequisite for the development of sustainable agricultural systems.

3.0 Designing and conducting on-farm surveys of resource-poor farmers' agricultural systems: a practical review[8]

3.1 Abstract

Agricultural research, administrative and extension staff working in developing countries often work with resource-poor farmers. These farmers' agricultural systems are markedly different from those of larger farmers. Farming systems research and extension (FSRE) approaches are popular for such work. On-farm surveys are a central component of FSRE but require design considerations and techniques not typical of the agricultural sciences. This practical review outlines experimental design and research technique considerations for on-farm surveys. General topics covered include historical antecedents, sampling techniques, interview design, interview administration, and a glossary of technical terms. Examples are used to illustrate the concepts and place them in a practitioner context.

3.2 Introduction

The Green Revolution (1960s) produced high yielding crop varieties and input intensive crop production systems (Clawson and Hoy, 1979), but neglected certain disadvantaged regions and farmers (Evenson and Gollin, 2003). Generally, resource-poor farmers in unfavorable farming environments have not benefited (Evenson and Gollin, 2003; Greenland, 1975; Merrill-Sands et al., 1991; Stroud, 1993), which is a concern because 450 million resource-poor farmers support 1.25 billion people, globally

[8] This chapter as developed by B.E. Love, L. Goonewardene, and D. Spaner has been published after non-peer review by the International Development Research Centre (IDRC).

(Mazoyer, 2001). Resource-poor farmers, here in refered to as poor farmers, are farmers whose resources (e.g. land, water, capital) do not permit a secure livelihood (Chambers and Ghildyal, 1985). Farming systems research and extension (FSRE) approaches were developed as a response to poor farmers not adopting Green Revolution technologies (Simmonds, 1986). Although the effectiveness of this approach has been questioned (Fielding, 1988; Herdt, 1987), and structural adjustment programs have reduced its priority (Finan, 1993), it remains a successful strategy (Collinson, 2000; Tripp, 1991).

On-farm surveys are a basic component of FSRE (Riley and Alexander, 1997; Simmonds, 1986; Stroup et al., 1993; Tripp, 1991), but the focus of agronomic literature has been on field trials (Ashby, 1986; De Groote and Traoré, 2005; Fielding and Riley, 1998; Hildebrand, 1984; Jones and Wahbi, 1992; Riley and Alexander, 1997; Tarawali and Pamo, 1992). Survey results are reported in agronomic research (Baidu-Forson et al., 1997; Schiere et al., 2000; Van Nieuwkoop et al., 1994; Wijeratne and Chandrasiri, 1993), but little direction on the practical aspects of designing and conducting surveys is available in agronomic journals. The techniques used to conduct on-farm surveys differ substantially from those used in field trials and draw heavily on the social sciences. Information on applying survey techniques is often not accessible to agricultural researchers because it is scattered throughout the social science literature.

Statistical analysis of on-farm survey data falls outside of the scope of this review. Many books and articles (Bernard, 2002; Chibnik, 1985; Cochran, 1977; Poate and Daplyn, 1993; Raftery, 2000; Trend, 1978; Yates, 1960) thoroughly review survey data analysis. Researchers are referred to these materials for coverage of statistical techniques. Likewise this review does not address surveying of farm physical attributes

(e.g. crop production, soils, livestock). Many texts and articles in the agronomic literature provide detailed information on procedures for physical sampling (Byerlee and Husain, 1993; Casely and Lury, 1981; Catchpole and Wheeler, 1992; Hume and Shirriff, 1995; Husch et al., 1982; Milner and Hughes, 1968; Mroz and Reed, 1991; Mueller-Dombois and Ellenberg, 1974; Poate, 1988; Poate and Casley, 1985; Poate and Daplyn, 1993; 't Mannetje, 1978; Wiegert, 1962) with the use of satellite information being the newest large-scale survey method available (Ippoliti-Ramilo et al., 2003; Murthy et al., 1996; Pinter et al., 2003; Reynolds et al., 2000; Silleos, 2002). The present review focuses entirely on practical aspects of experimental design and research techniques for preliminary on-farm surveys. No review of on-farm surveys can be exhaustive, but rather may be used as a starting point for topic specific reading.

3.3 Preliminary on-farm surveys

Use of surveys to gain initial understanding of agricultural systems is important (Simmonds, 1986) and permits hypothesis development (Settle et al., 1996). Surveys obtain information about agricultural systems through interviews (Abeyasekera et al., 2002; Ashby, 1990; Baker et al., 1988; Campbell and Stone, 1984; Rhoades, 1985). Interview surveys can be classified based on a number of criteria, including: 1) form of administration (verbal versus written, individual versus group), 2) type of interview (structured versus unstructured), 3) use of time and informants (repeated surveys versus one-time surveys).

3.3.1 History

Traditionally, preliminary on-farm studies have employed formal survey methods (e.g. Poate and Daplyn, 1993); however newer methods have been developed. Rapid rural appraisal (RRA) (Carruthers and Chambers, 1981) methodology came about, in part, as a response to the ineffectiveness of costly large-scale formal surveys that often produced misleading, difficult to use, and largely ignored results (Chambers, 1994a). Participatory rural appraisal (PRA) evolved out of RRA because rapid techniques were not inclusive (Mascarenhas, 1991).

Rapid Rural Appraisal and PRA approaches shifted survey techniques from: outsider (researcher) to insider (farmer) explanations, measuring to comparing, closed to open questions, individual to group interviews, and verbal to visual interactions (Chambers, 1994b). Chambers reviewed the origins (Chambers, 1994a), experiences (Chambers, 1994b), and challenges and potential (Chambers, 1994c) of PRA and suggested that it is an improvement over RRA. Few manuals on RRA/PRA methods exist, due to the perception that common sense should guide the researcher (Chambers, 1994a), but Chambers (1994a; 1994b) and Mascarenhas (1991) outline common PRA techniques. Despite these shifts, formal survey approaches remain important.

3.3.2 Experimental design

Surveys can be either descriptive or comparative (Oppenheim, 1992). Data from descriptive surveys can be used after their collection to conduct comparisons. For instance, comparing farm management and productivity between poor farmers holding land title versus those without. Issues of sampling and measurement apply across all

survey types. Sampling requires a definition of the individual units that are to be sampled (e.g. households, farmers) and the population they belong to (e.g. all farmers in a certain region, all farmers receiving credit) (Poate and Daplyn, 1993). Databases of these units for the population of interest (e.g. registry of farmers, satellite images of farms) are required for sample selection. These databases are often incomplete and/or inaccurate (Alreck and Settle, 1995). Agricultural surveys use both area databases (agricultural land) and list databases (known farmers) (Yates, 1960). List databases tend to be incomplete but more efficient for sampling farms (Chhikara and Lih-Yuan, 1992). For example, a list of farmers obtained from a local extension agent is likely to be incomplete compared to a satellite photo of the area, but is much easier to use.

Sample size is influenced by whether a survey is descriptive or comparative. Descriptive studies aim to provide accurate estimates of population attributes (e.g. income, yield). The required sample size depends on: 1) the heterogeneity of the population, 2) the number of factors studied, 3) the size of the investigated attribute, and 4) the desired level of precision for the estimate (Bernard, 2002). Cochran (1977) outlined mathematical formulas for determining sample sizes and on-line sample size calculators are available[9]. Rapid rural appraisal techniques often use very small samples that violate statistical norms for survey sample sizes (Carruthers and Chambers, 1981). When presenting results based on RRA techniques, researchers must be careful not to suggest the statistical rigor that only larger sample sizes can achieve. These small samples may be justified as optimizing trade-offs between accuracy, relevance, timeliness and cost (Carruthers and Chambers, 1981). For example, a pilot extension program for

[9] For proportions: http://www.surveysystem.com/sscalc.htm; http://www.raosoft.com/samplesize.html

poor farmers that needs to use funds by the end of the fiscal year may conduct a small survey lacking precision and accuracy, but which meets program deadlines.

When comparisons rather than estimates are required, sample sizes are determined by: 1) the statistical test being used, 2) the variability in the compared populations, 3) the size of the difference to be detected, 4) and the desired probabilities of detecting true and false differences (Sokal and Rohlf, 1995). Zar (1999) provides formulas for sample size calculation for many statistical tests and on-line sample size calculators are available for some statistical tests[10]. The information used for sample size calculations is determined by the objectives of the experiment (type of comparison: test used) and the judgment of the researcher (e.g. desired precision, probabilities of errors, and difference size).

The probability of detecting a false difference or failing to detect a true difference are referred to as type I (α) and type II (β) errors, respectively (Neyman and Pearson, 1928). Power is the probability that a true difference will be detected and is given by $1 - \beta$ (MacDonald, 1999). Traditionally, an α of 0.05 has been used (Sokal and Rohlf, 1995), but α-value selection is subjective and requires researcher judgment (Lauckner, 1989; Neyman and Pearson, 1928). Appropriate α-values are determined in part, by the seriousness of committing different types of errors (Carmer and Walker, 1988). Shrader-Frechette and McCoy (1992) argue type I error prevention is preferred by pure science (preference for failing to acknowledge a truth over accepting a falsehood) and type II error prevention is preferred for applied science (preference for avoiding harm or loss of benefit). Agriculture is an applied science and therefore may reduce type II errors (i.e.

[10] http://www.changbioscience.com/stat/ssize.html;

increase power) by employing larger α-values (Carmer, 1976). This occurs because the power of a test is proportional to the test's α-value (Thomas and Juanes, 1996).

Power can be assessed for many statistical tests (Zar, 1999) but not all (Castelloe, 2000). Defining high power is somewhat arbitrary but values of 0.8 to 0.95 are generally considered acceptable (Thomas and Juanes, 1996). If the power of a test is deemed to be too low, for a given α-value, sample size may be increased (Sokal and Rohlf, 1995). However, very large sample sizes increase power to the point where statistical significance can be demonstrated in most cases, while small-sample sizes may fail to detect biologically important differences (Thomas and Juanes, 1996). Both researchers and farmers desire biologically meaningful results (Borel and Romero, 1991). Cohen (1988) provides power analysis suggestions to ensure that sample sizes are adequate for detecting biologically important effects.

Variability and attribute size estimates, for calculating sample size and power, may be based on researchers' best guesses (Bernard, 2002), past studies (Gomez and Gomez, 1984), and/or pilot studies (Cochran, 1977). A practical situation might involve researchers reviewing existing literature and studies, discussing their personal perceptions, and arriving at educated estimates for attribute variability. This information could then be used to calculate required sample size. If the required sample is unacceptably large a more achievable sample size can be selected and its power evaluated.

3.3.3 Sampling techniques

There are many techniques for sampling populations. Simple random sampling is a form of probability sampling where each unit in a population has an equal probability of being selected. This permits the generalization of survey's results to the population being studied (Oppenheim, 1992). Prior knowledge of population attributes allows division of sampling units into groups, prior to random sampling, which can improve efficiency and is termed stratified random sampling (Neyman, 1934). For instance, a study of farmers in a given area should not randomly sample all individuals if the research objective is to compare those receiving extension assistance with those who do not. Rather, the study should divide farmers into the groups they belong to and then take random samples from each group. Sampling within groups may be proportional to group sizes, the same for all groups, or different for each group (Poate and Daplyn, 1993). Sampling in proportion to group size makes calculation of population attributes easier (Cochran, 1977). Equal sampling provides a balanced design for comparisons (Zar, 1999). Different sample sizes may improve efficiency when variability in attributes differs between groups (Yates, 1960) because groups with low variability do not need to be sampled as much to achieve the desired precision. For example, an on-farm survey comparing cropping practices in two regions may attempt to sample an equal number of farms from each region. However, if one of the regions is more variable agroecologically and precise estimates rather than comparisons are desired a larger sample may be required for the more variable region.

Simple random and simple stratified random sampling, require accurate databases to sample from. Sample size should reduced by up to on third in order to release funds

for constructing appropriate databases for large-scale surveys (Scott, 1985). One useful method for database construction is sampling at a number of sequential levels using existing databases (e.g. provinces, counties, towns) and then conducting a census to obtain a database for sampling (Poate and Daplyn, 1993; Bernard, 2002). If a census is deemed too expensive this sequential approach may sample smaller and smaller groupings until the unit of interest is obtained (Scheaffer et al., 1979). In the field a researcher may use geographical maps to select valleys, followed by a town list to sample towns, and subsequently town maps to choose houses from which farmers can be picked for interviewing. The final desired sampling unit is defined by a study's objectives. For instance, a survey of farmer activities will sample farmers, while a survey of women's role in agriculture will sample women living in farming communities or households.

Generally units from the same group are more alike than units from different groups (Wooldridge, 2003). Thus, sampling a few units from each of a large number of groups is preferred (Stoker and Bowers, 2002). For example if a survey sampled groups of towns and then farmers within towns, the best strategy may be to select many towns and relatively few farmers per town. Generally, at least 5 households should be sampled per group (Bernard, 2002).

Rural appraisal techniques often use purposive (intentional selection of informants) rather than probability sampling (Mascarenhas, 1991). This is because the studies seek to examine a number of factors, and the populations under study are often scattered and are not recorded in databases (Carruthers and Chambers, 1981). Bernard (2002) describes a number of non-probability sampling techniques. He notes that while they produce biased population estimates they are less costly and can be useful for 1)

gaining information on issues to be studied (convenience sampling), 2) studying social networks and building databases (snowball sampling), 3) providing a similar control group (case control sampling), and 4) collecting cultural data (key informant sampling). Bias can be assessed in part by comparing sample attributes (age, education) to past census data for the same population (Smith et al., 1991).

Generally, farmers in developing countries are more diverse in terms of their management (Crossa et al., 2002) and environments (Hildebrand, 1984) than farmers in developed countries. Findings for one group may not apply to another group or specific sub-groups (e.g. poor farmers as opposed to all farmers in a given area). These differences may be because poor farmers manage their farms differently due to dissimilarity in resource access. Errors introduced by these grouping effects can be adjusted for statistically but cannot be eliminated (Steel and Holt, 1996).

Alternatively, defining relatively uniform groups gives results specific to the groups being studied, which makes result extrapolation easier and more accurate (Franzel, 1992). These groups can be constructed using multivariate empirical procedures (Freeman et al., 2002), non-local experts (agronomists, scientists) (Wotowiec et al., 1987), or local experts (farmers) (Ashby, 1990). Employing local experts is advantageous because it is quick, inexpensive and helps develop researcher farmer relationships (Franzel, 1992). In the past, groups have been defined by environmental variables (Gomez and Gomez, 1984). More recently, socio-economic variables (Crossa et al., 2002) and management practices (Wotowiec et al., 1987) are being considered. Using socio-economic data is important because poor farmers behave differently from other farmers even if they share similar environments (Netting, 1993).

3.4 Surveying people: interviews

Interviews are used to gather information from people. Issues surrounding interviews include: interview structure, question wording, questionnaire organization, and interview environment.

3.4.1 General interview structure

Interviews may be informal, unstructured, semi-structured or structured. Informal interviews consist of a researcher trying to remember conversations and taking notes after relevant interactions (Bernard, 2002). For instance, an extension agent may record their observations from field visits and farmer interactions at the end of each day. Unstructured interviews have a topic of interest but do not explicitly direct informants, in order to encourage openness, expression, and discovery (Sjoberg and Nett, 1968). Semi-structured interviews are guided by a list of questions/topics that need to be covered but allow interviewers to ask follow-up questions based on informants' responses (Arksey and Knight, 1999). Structured interviews attempt to get informants to respond to a uniform set of stimuli (lists of questions in a particular order) (Labaw, 1980).

In practical terms an unstructured interview might ask farmers to discuss the general topic of maize, whereas a semi-structured interview would specifically ask farmers to talk about the characteristics of different maize varieties, management of maize fields, and commercialization of maize products. A structured interview would involve specific questions such as 1) "Do you grow maize?", 2) "What maize varieties have you planted this year?", 3) How much of each type?", 4) "How much maize did you

sell last year? 5) At what price?"; all asked in a specific order. Traditional agricultural surveys use structured interviews (Poate and Daplyn, 1993). Rural appraisal methods prefer the other forms of interviewing (Carruthers and Chambers, 1981). Structured interviews are useful when the study objectives are narrow and well defined (Oppenheim, 1992) such as agricultural censuses for government planning.

In many cases surveys for on-farm research are conducted to study a situation that is not well known (Chambers, 1994b) making flexibility data collection rather than uniform specific data collection desirable (Rhoades, 1985). Prior to administering an interview some ethical issues must be addressed. Respondents' anonymity and confidentiality should be assured, the nature of the interview clearly explained, and permission requested (Bernard, 2002). This can be accomplished in part by using a permission form that outlines respondent rights and obligations (Seidman, 2006).

3.4.2 Interview questions

Questions and their organization are fundamental components of interviews. Good questions contribute more to accuracy than sampling methods and should be simple, understandable, bias-free, and not irritating (Payne, 1973). In practical terms, the question "Do you plant trees in your pasture?" is superior to "So it is my understanding that you practice agrosilvopastoralism, this is correct, right?", which is complicated, employs an uncommon term, and biases the respondent towards positive responses. Each question should focus on a single topic (Alreck and Settle, 1995) and important topics can be identified by reviewing relevant literature (Arksey and Knight, 1999).

Questions may be open-ended or closed, with the former either permitting any response or selection from a list of possible responses (Alreck and Settle, 1995). For example, a farmer may be asked to select from a list, the crops he farms, or alternatively state the crops he farms without using a guide. A series of closed-ended questions may be employed instead of open-ended questions e.g. "Do you plant maize? Do you plant rice?", but is time consuming.

Generally, questions should: have a single meaning, use simple understood vocabulary, have a clear purpose, provide appropriate alternatives, and not be leading (Canada, 1995). Questions should be short unless threatening or sensitive (Bernard, 2002). Threatening questions (e.g. land and livestock ownership) result in underreporting (Sudman and Bradburn, 1974), but estimates can be adjusted by assessing threat perception (Bradburn et al., 1978). Techniques for asking sensitive questions include: using open-ended questions and suggesting the sensitive behavior or situation is common (Arksey and Knight, 1999). For example, a question about fire control in slash-and-burn agriculture might acknowledge the difficulty of controlling fire before enquiring if an informant has burned adjacent forest.

The key to successful unstructured and semi-structured interviewing is deeper inquiry about informants' responses (Bernard, 2002). Inquiry can be accomplished in many ways. For instance repeating the last thing said, "So, harvest occurs mid-April, what happens next?", asking the informant to tell more, "Please explain more to me about that", or simply silence (Canada, 1995). Interviewers must be careful that their inquiries do not lead informants to specific answers (Houtkoop-Steenstra, 1996).

Labaw (1980) argues that questionnaires aimed at predicting behavior (e.g. technology adoption) should focus on informants' environment, knowledge, and actual behavior because attitudinal questions reveal little about future behavior. In practice this means asking a farmer about planted crops, available home labor, knowledge of organic fertilizers, and actual use of organic fertilizers, rather than inquiring whether a farmer believes organic fertilizers are useful and should be used.

Opinion questions often use ranking or scoring (Anderson, 1976). Ranks place items in order while scoring assigns points to items. Farmer preferences can be evaluated with these techniques (e.g. Ashby et al., 1987; Bellon, 1996; del Pilar Guerrero et al., 1993). Ranking can be made easier by sorting cards (Ashby, 1990), where informants place cards representing items (e.g. crops, livestock, fertilizers) in order according to their rank. Ranking of all pairs of items one at a time makes ranking easier for farmers (Fielding et al., 1998), but comparison of more than 6 items is laborious (Ashby, 1990).

Ranking does not provide information on the magnitude of the gaps between ranks, which prevents evaluation of relative preference (Maxwell and Bart, 1995). Preference evaluation techniques should allow ties and extreme values, and be easy to administer (Fielding and Riley, 2000). Ranking fails the first two criteria, whereas scoring meets all three requirements when five times as many points as items are used (Fielding and Riley, 2000), but can be excessively time consuming (e.g. Abeyasekera et al., 2002) and require greater explanation (Converse and Presser, 1986). Maxwell and Bart (1995) describe a number of different types of scoring. In practice, a researcher might ask a farmer to place five cards with pictures of crops in order of their importance,

a form of ranking. However, it would be preferable to have the farmer distribute 25 stones among the cards based on their importance, a form of scoring.

3.4.3 Interview organization

Interview organization is also important. The format of a structured interview should 1) prevent bias due to question order, 2) flow smoothly, 3) be easy to follow for the interviewer, and 4) be efficient for data entry (Labaw, 1980). The order of questions can alter responses (Noelle-Neumann, 1970; Schuman et al., 1983). Use of relatively neutral questions preceding sensitive questions can improve the truthfulness of responses (Thumin, 1962) and can also help in situations where a preceding question alters the response to a subsequent question (Schuman et al., 1983). For instance a researcher would inquire about the type of crops planted and their management before asking more sensitive questions about farm size and title status.

Grouping like questions together can affect responses, but randomly dispersing questions can frustrate informants (Metzner and Mann, 1953). Generally, grouping similar questions into sections (e.g. farm attributes, farm management) is best (Alreck and Settle, 1995). Simple factual questions, such as background information, should be asked first (Phillips, 1981). Overly long interviews reduce the quality of responses (Burchell and Marsh, 1992), but what is too long is partially dependent on respondents' interest (Herzog and Bachman, 1981). Overall, balance is required when designing surveys with regards to length, repetition, and ordering of questions. Generally, interviews with poor farmers should be no longer than one hour, questions should be grouped based on content, and non-personal factual information questions should be

asked first. If the survey topic is of great interest or importance to respondents, interviews may be longer.

Interview questions often lead into each other in a logical order. For instance questions about crops being grown subsequently lead to specific questions about particular crops. Structured interviews can use specific questions first to filter informants that do not need to be asked subsequent questions (Alreck and Settle, 1995). For example asking an informant if they have received a loan is required before asking how much they were loaned or by whom. The interview form an interviewer reads can use numbering, indenting, and font options to guide the interviewer through related series of questions (Labaw, 1980). Using numbers to record predetermined responses is quicker than writing down full-responses (Alreck and Settle, 1995). Using a tape recorder is an alternative and can be very useful for interviews that have less structure (Bucher et al., 1956). However, transcription quality can be problematic as well as costly (McLellan et al., 2003) and tape recorders may not be acceptable to all informants (Bernard, 2002). Poorly organized interviews take substantially longer to obtain the same information (Phillips, 1981).

3.4.4 Interview physical and social setting

The physical and social setting of interviews influences informants' responses (Briggs, 1986) and deception during interviews can be a problem (Malton, 1983). For example, some national agricultural census publications are prefaced with a warning about accuracy due to deception (Contraloría, 2001b). Prepaid non-monetary incentives can increase response rates and improve response completeness (Willimack et al., 1995).

Active involvement of informants (e.g. card sorting), reduces monotony and can result in improved responses (Noelle-Neumann, 1970).

Responses may be affected if the interviewer is of a different ethnic group, especially when informants are of low-income status (Schuman and Converse, 1971). Foreign researchers may choose to train local people to conduct interviews (Stycos, 1952) in order to address this issue. Training quality affects survey results (Billiet and Loosveldt, 1988) making significant investment in training necessary. Interviewer gender can influence responses (Kane and MacCaulay, 1993). Traditionally, women have been ignored as interview subjects (Reinharz and Chase, 2002). However, women's roles in agricultural systems are fundamental ones (Boserup, 1971). As such, female interviewers can be particularly important when investigating women's roles in agricultural systems.

Group interviews are a special case that involves generating discussion amongst several people and recording their responses. Often four to six different group sessions are needed to obtain the desired information, with groups of more diverse individuals providing more information (Morgan, 1996). Smaller groups with seven to eight participants are preferable because they are manageable without being dominated by a few opinionated individuals (Bernard, 2002). Group interview moderators need to be well trained in generating open discussion (Powell and Single, 1996). Group interviews can inhibit individuals and result in false consensus but are productive for exploratory and feedback work (Ashby, 1990). An example of group interviewing for agronomic purposes is inviting several farmers to discuss their preferences for different crop varieties (Ndjeunga and Nelson, 2005).

Interviewing informants after events occur can result in altered information due to forgetfulness or placing of events before or after they actually occurred (Neter and Waksberg, 1964). Usually informants report events as having occurred more recently than is the case (Neter and Waksberg, 1964; Sudman et al., 1984). Recalling events can be made more accurate by breaking time into a number of smaller periods. For multiple interviews the visit schedule defines the time periods, while for one-time interviews time periods must be verbally defined before each set of questions.

Verbally defining time periods can be made more accurate by relating time periods to major events such as local celebrations or births and deaths (Martyn and Belli, 2002). For instance asking, "So the first weeding occurred a week before the town's patron saint celebration?" helps confirm timing. In multiple visit interviews longer time periods are more resource efficient but intervals greater than one month result in events being forgotten (Neter and Waksberg, 1964). Interviewing farmers in their fields can also improve responses (Chambers, 1994a) because the field environment provides a physical cue for memory recall when answering questions. Visits must be appropriately timed (e.g. planting, weeding, harvesting) to facilitate recall (Ashby, 1990). Two to four well-timed visits during the period of interest (e.g. growing season, livestock herding) are thought to be adequate (Byerlee and Triomphe, 1991; Versteeg and Huijsman, 1991). Timely visits are difficult to make and extra visits are usually required to ensure contact (Stroud, 1993). Excessive contact can inconvenience participants and result in dropouts (Oppenheim, 1992). Obtaining more accurate information must be weighed against the costs of more frequent contact.

3.5 Pre-testing surveys

Prior to large-scale administration of a survey it should be pre-tested. Pre-testing surveys involves applying the survey with a small sample (20-25 informants) in order to assess the appropriateness of the survey design and techniques (Singleton and Straits, 2002). Survey pre-testing can reveal problems before they become unmanageable at larger scales (Cochran, 1977). Oksenberg et al. (1991) review pre-testing's rationale, implementation, and recent improvements. Pre-tests evaluate individual questions as well as overall interview organization (DeMaio and Rothgeb, 1996). Pre-tests should be conducted under conditions identical to those of the actual survey and informants used for the pre-test must not be used later in the actual survey (Oppenheim, 1992).

3.6 Conclusions

Preliminary surveys are a fundamental component of on-farm agricultural systems research. Unlike standard laboratory and on-station agricultural research, on-farm surveys draw heavily on the social sciences and must confront the practical constraints of working with farmers. This review outlines some practical approaches for addressing common problems but is not exhaustive. Practitioners are encouraged to review the references and engage in further topical reading prior to conducting surveys. A glossary of technical terms is provided to help researchers search within the applicable social science literature (Appendix 3.1).

4.0 Collection and characterization of maize and upland rice populations cropped by subsistence farmers in the uplands of Panama's Azuero region[11]

4.1 Abstract

Conservation of crop genetic resources is an international priority and requires continued collection and characterization of farmer varieties. We collected and characterized maize and upland rice populations cropped by farmers in Panama's Azuero region. The objective of our study was to evaluate the crop genetic diversity of farmer varieties of maize and upland rice grown by subsistence farmers in Panama. We found: 1) farmers' naming practices only partially corresponded to genetic relationships and were strongest for rice populations, 2) farmers' classification of populations as "modern" or "traditional" was reflected in phenotypic differences, 3) Panamanian maize populations were molecularly distinct from populations collected elsewhere in Latin America, and 4) heterogeneous rice populations were common and heterogeneity was often due to admixture of recognized farmer varieties. Our results indicate subsistence farmers in Panama continue to farm traditional varieties but there has been substantial adoption of "modern" varieties.

4.2 Introduction

Conservation of plant genetic resources is a global priority (FAO, 1998). Maize and rice have been extensively collected (Plucknett et al., 1987), but further collection is

[11] This chapter, as developed by B. Love, S. Dreisigacker, and D. Spaner, has been submitted to *Genetic Resources and Crop Evolution*.

warranted (Appa-Rao et al., 2002; FAO, 1998). Subsistence farmers often retain high levels of crop diversity (Maxted et al., 2002).

In Panama, rice (*Oryza sativa* L.) and maize (*Zea mays* L.) are the primary staple crops (McKay, 1990) and swidden agriculture (cycling between long fallows and short cropping periods in which fire is used to clear fallow land) is common (Fischer and Vasseur, 2000). Panama was the bridge over which maize passed from its centre of origin (Mexico) into maize's largest centre of diversity (South America) (Freitas et al., 2003). Panama is also adjacent to the first reported place of rice cultivation in the New World in 1517, and served as an early port for rice trading (Spijkers, 1983). Natural genetic diversity in Panama is elevated due to high levels of environmental heterogeneity (Condit et al., 2002).

Rice (Lawrence, 1984) and maize (Kuleshov, 1930; Lawrence, 1984) collections in Panama have been limited and further collection is funding-dependent and opportunistic (CNRFP, 1995). The germplasm bank of the International Maize and Wheat Improvement Center (CIMMYT) harbors few Panamanian maize accessions. CIMMYT maize germplasm records (Taba et al., 2003) indicate most Panamanian accessions date back to 1958 and only a few are from Panama's Azuero region, the heartland of Panamanian agriculture (Jaen-Suarez, 1978). National collections of maize and rice are also limited, consisting of only a few hundred accessions each (CNRFP, 1995).

Farmer nomenclature can obscure the relationships between populations (Bellon, 2004) and heterogeneous populations of self-pollinating crops are common (Smale et al., 1998). Notions of "modern" and "traditional" germplasm are often not well defined,

especially in the case of open-pollinated crops (Louette, 1999). The term "modern" is typically used to indicate materials have been improved by formal plant breeding, whereas "traditional" indicates that farmers have managed materials with or without improvement. Characterization of collected germplasm is required before it can be incorporated into a breeding program (Marshall and Brown, 1975). The objective of this study was to characterize the crop genetic diversity of maize and upland rice cropped by subsistence farmers in Panama. The study provides baseline information on diversity and phenotypes and their relationship to farmers' classifications.

4.3 Materials and methods

4.3.1 Study Site

The study was carried out in Panama in the tropical forest uplands of Herrera province (Azuero region) where subsistence farmers continue to practice swidden agriculture. The climate is wet (2000mm $year^{-1}$) and warm (25°C) and cropping occurs almost exclusively during the rainy season. Steep erosion-prone hills dominate the uplands where both maize and rice are grown in dryland conditions. The natural vegetation type is tropical forest, and fallow fields resemble pioneer or secondary forest before being slashed-and-burned for agricultural production.

4.3.2 Collection strategy

Towns in the upland zone, which were accessible by local transport and no more than three hours walking distance, were stratified on the basis of agricultural practice (swidden and transition from swidden to permanent plot agriculture). Five towns were

randomly selected from each of these two strata. Public meetings were held in each town to recruit farmer participants in December 2004. Farmers attended the meetings voluntarily and those who were interested signed up for the collecting mission. Farmers from nearby towns who attended the meetings were also allowed to participate. Participating farmers were asked to share seed from up to 50 rice panicles and 50 maize ears for each population they farmed. The study defined a population as a group of plants or seed managed by a given farmer as a distinct variety.

A structured interview[12] lasting ~10 minutes was administered to collect passport data. Specifically, farmers were asked to identify each population by name, indicate whether each population was considered "modern" (i.e. the product of a crop improvement program) or "traditional" (i.e. not the product of a crop improvement program), and specify whether they practiced swidden agriculture or were making a transition to permanent plot agriculture. Farmers that provided rice populations which exhibited heterogeneity during population characterization were visited again and questioned about the origin of the heterogeneity using an unstructured interview lasting ~10 minutes. Seed from each panicle and ear was packaged separately, treated for insect pests with phosphorous hydride, and stored.

4.3.3 Morphological characterization

Populations for which sufficient seed was collected were characterized in an agromorphological trial in Panama's lowlands. The trial employed a randomized complete block design consisting of two replicates. The soil at the trial site was a clay

[12] The interview process received ethics approval, and informed consent was obtained from all informants prior to asking interview questions.

loam of light yellow colour with a pH of 5.6 and an organic matter content of 2% and uniform in appearance. Site topography was flat and prepared by mechanical tillage. The area has an average annual rainfall and temperature of 2000mm and 27°C, respectively (IGNTG, 1988). All plots were hand seeded in the second week of July 2005, using a seeding density of 106/m^2 in three rows (30cm x 30cm) for rice and a seeding density of 4.7/m^2 in two rows (75cm x 30cm) for maize. Trial conditions differed from slash-and-burn agriculture in that the soils were richer, climate was slightly warmer, planting density was higher, and chemical fertilizer was used instead of ash. Still, the trial site was similar in climate, and the practice of dry land planting (i.e. hand seeding, and manual weeding) mimicked typical farmer practice.

One certified variety was planted for both maize (Guararé) and rice (Orisíca) as a check. Commercial farmers grow cv. Guararé throughout Panama and Ministry of Agriculture extensionists encourage upland rice farmers to plant cv. Orisíca. Certified seed of both check varieties was obtained from Panama's Institute for Agricultural Research (IDIAP). At planting, 100Kgha^{-1} of 12-24-12 (NPK) was applied by drilling and 50 Kgha^{-1} of urea (46-0-0) was applied three weeks after emergence by top-dressing. Weeds were controlled manually and insect pests were controlled with a single spraying of (RS)-ciano-3-fenoxibencil (1RS,3RS;1RS,3SR)-3(2,2-diclorovinil)-2,2-dimetilciclopropano carboxilato 6.00% at a rate of 9ml L^{-1}. A total of 57 and 49 traits were measured for maize (described in IPGRI, 1991) and rice (described in FAO, 1980), respectively. Traits included nominal (colors, presence of botanical features, and type of growth habit), discrete (counts of botanical features, e.g. ears), and continuous (measurement of botanical features e.g. heights, weights) variables (Tables 4.1 and 4.2).

All weight metrics were adjusted to 12% moisture content for maize and 10% for rice for comparison.

4.3.4 Molecular characterization

Only the maize populations were characterized at the molecular level. Maize genotyping was done in CIMMYT's Applied Biotechnology Center using a bulked DNA technique for microsatellites (Dubreuil et al., 2006; Warburton et al., 2001). In brief, the molecular methods (Figure 4.1) included: 1) collection of tissue samples from 15 randomly selected individuals from each population grown under greenhouse conditions, 2) extraction of DNA from individual leaf tissue samples using a modified CTAB method (CIMMYT, 2005) based on Saghai-Maroof et al.'s (1984) protocol, 3) quantification of individual DNA samples using a Nanodrop® ND-1000 spectrophotometer (Nanodrop, Wilmington, DE), 4) bulking of equal quantities of DNA from each of the 15 individual samples belonging to a population to form a population DNA bulk, 5) allele amplification using selected fluorescently labeled microsatellite primers (Appendices 4.1 and 4.2), 6) detection of amplification products using an ABI^{TM}3100 sequencer (Perkin Elmer/Applied Biosystems, Foster City, CA), 7) identification of amplified alleles and correction of allele size, if necessary, on the basis of control samples using GeneScan® (Applied_Biosystems, 2001) and Genotyper® software, 8) estimation of allele quantities based on fluorescence intensity (maximum peak height) and calculation of allele frequencies using mathematical procedures described in Dubreuil et al. (2006) implemented with R software, and 9) grouping of detected alleles into allele categories on the basis of marker repeat size and alleles detected in past studies.

Eleven microsatellite markers, spread across the maize genome that had been optimized for amplification in bulk DNA samples, were used for genotyping. The microsatellites are publicly available (http://www.maizegdb.org/) and were: phi063, phi065, phi079, phi102228, phi299852, umc1161, umc1196, umc1447, umc1545, umc1917, and umc2250. Microsatellite data for the same marker set, with the exception of phi065, were obtained for nine populations (from various parts of Latin America) that are used as diversity standards by the Applied Biotechnology Center at CIMMYT. These diversity standards were collected between 1943 and 1970 from Peru, Ecuador, Bolivia, Cuba, and Mexico at altitudes ranging from 30 – 2700 m.a.s.l. Four of the nine populations are of Mexican origin while all other countries are represented by a single population.

4.3.5 Statistical analysis

Descriptive statistics were used to evaluate the occurrence of morphological characteristics in heterogeneous rice populations. Analysis of variance was used to compute phenotypic values for the traits of farmer varieties. Cluster analysis (Gower's distance, Ward's linkage method) (Struyf et al., 1997) was used to visualize populations' relationships on the basis of phenotypic data for rice and both phenotypic and molecular data for maize. Ordination (Euclidean distance, Non-metric multi-dimensional scaling) (McCune and Grace, 2002) was employed to visualize relationships for CIMMYT diversity standards and Panamanian maize populations on the basis of molecular data only. A multiple response permutation procedure (Mielke and Berry, 2001) was utilized to assess the relationship between populations and grouping variables. Two grouping

variables were considered: 1) varietal identity ("modern" or "traditional") and 2) farming practices (swidden versus transition).

A Bonferonni-adjusted mixed model analysis was used to evaluate which phenotypic traits differed for different levels within groups and to estimate least-squared means for traits. Straight-line geographical distances between collection site centroids were computed for all populations and a mantel test was used to correlate geographical distances with genetic distances. PC-ord (McCune and Mefford, 1999), SAS system (SAS, 2005), and R (R_Development_Core_Team., 2007) statistical software was used to implement the above statistical procedures.

4.4 Results and discussion

Fifty-seven farmers provided a total of 71 maize populations and 54 rice populations belonging to 10 and 20 distinctly-named farmer varieties, respectively (Figures 4.2 and 4.3). Sufficient seed for a phenotypic characterization trial was available for 46 maize populations and 52 rice populations as well as the check varieties. Additionally, the 46 maize populations and the check variety were characterized at the molecular level.

Off-types were identified in 37% of rice populations on the basis of seed morphology. In 68% of these cases, the farmers providing the seed indicated that off-types were the result of admixture between recognized farmer varieties. In the other cases, off-types were deemed to be of the same farmer-variety that had been collected. Thus, on the basis of seed morphology, we found farmers only sometimes (32%) declare a heterogeneous population to be a single variety. Varying percentages of collected rice

populations exhibited heterogeneity for other qualitative traits: awns (63%), leaf pubescence (21%), leaf sheath colour (12%), collar colour (8%), node colour (4%), internode colour (4%), and anther colour (2%). In contrast to heterogeneity in seed morphology, no farmers indicated heterogeneity in these traits was the result of admixture. The results indicate that heterogeneous upland rice populations appear to be common in Panama and, while farmers often recognize heterogeneity to be the result of admixture where grain traits are concerned, they tend to lump variants together into a single farmer variety where other forms of heterogeneity are concerned.

Ranges indicated that maize populations were uniform for flowering, silking, anthesis and maturity but exhibited a wide spread for ear height, secondary tassel branching, leaves above the ear, ear diameter, cob diameter, cob rachis diameter, husk weight, cob weight, 100-grain weight, ear yield, and yield (Table 4.1). In contrast, rice populations were more uniform for most variables and only panicle length and yield had a wide spread. Selected nominal traits for maize and rice (Table 4.2) exhibited significant variation. For maize, high levels of uniformity were only apparent for tillering and pubescence. In contrast, rice exhibited uniformity for a slightly larger number of traits: collar color, auricle color, ligule color, ligule type, panicle branching, and seed coat color. Higher levels of uniformity in rice may be due to the greater genetic isolation of self-pollinated crops as well as the possibility of a genetic bottleneck upon introduction to the New World.

Farmers' naming practices only partially agreed with cluster analysis results and were strongest for rice (Figures 4.2 and 4.3). The agglomerative coefficient for rice clusters (0.86) was higher than that of maize (0.68). Discrepancies between farmer

nomenclature and statistical clustering are likely due to farmers using a few key characteristics (e.g. husk or hull colour, maturity) to classify populations while cluster analysis uses a large number of characteristics to evaluate cluster membership. As such, populations of the same name belonging to different clusters are evidence of variation existing within farmer varieties as well as some misclassification. The higher agglomerative coefficient of rice indicates that its clusters are more distinct than those of maize and this may be expected for a self-pollinating crop compared to an open-pollinated crop.

Ordination of the molecular data explained 68% of the variance in the data (Axis 1 = 42%, Axis 2 = 26%) and indicated Panamanian maize populations were largely distinct from CIMMYT's diversity standards with the exception of an Ecuadorian population. Panamanian populations were also fairly similar to each other (Figure 4.3), compared to similarity between the diversity standards. It is unclear whether the detected differences are related to temporal or geographical distinctness. Interestingly, the diversity standard that was most similar to Panamanian populations was collected at an altitude of 2200 m.a.s.l in Ecuador.

Despite this difference in altitude, Ecuador shares a long history of migration and interconnectedness with Panama (Kolman and Bermingham, 1997). Greater similarity within Panamanian populations compared to the diversity standards is expected given the temporal and spatial similarity of Panamanian populations to each other. This molecular distinctness suggests molecular diversity of interest may exist in Panamanian populations (Appendix 4.3). Mantel tests comparing the geographic distance between population collection sites with genetic distance between populations were not significant for either

rice or maize. This suggests that over the small geographical distances involved in this study (<40 Km), genetic distance was not correlated with geographical distance.

Multi-response permutation procedures indicated a grouping effect on the basis of populations' having a "modern" or "traditional" identity for both maize ($p = 0.01$) and rice ($p < 0.001$) based on phenotypic data. However, no grouping effect was found for molecular data on the basis of "modern" or "traditional" identity for maize ($p = 0.29$). Nor was a grouping effect detected for farm management (swidden agriculture versus transition) for either maize ($p = 0.50$) or rice ($p = 0.15$). This indicates that while differences in phenotypic traits are associated with notions of "modern" or "traditional", this is not the case for type of management. Swidden agriculturalists and those in transition to permanent agriculture appear to be cropping populations with similar suites of phenotypic traits. That "modern" and "traditional" effects are not detected in the molecular dataset is unsurprising given the use of a small number of selection neutral markers. Furthermore, gene flow can obscure differences between open-pollinated varieties at the molecular level (Louette, 1999).

A total of 13 and 6 phenotypic traits were significantly different between populations with "modern" and "traditional" identities for maize and rice, respectively (Table 4.1). In the case of maize, greater 100-grain weight, earlier silking, lower ear to plant height ratio, greater grain yield per ear, and smaller tassels for populations of "modern" identity is consistent with trends in modern maize breeding programs (Duvick, 2005). Higher grain yields per ear did not translate into higher yields per hectare because "traditional" farmer varieties tended to have a greater number of ears per plant. In the case of rice, shorter-narrower leaves, higher 100-grain weight, earlier flowering, and

higher yield was consistent with objectives in modern rice breeding programs (Peng et al., 1999). This suggests farmers' notions of "modern" and "traditional" parallel changes in plant morphology being driven by modern breeding programs.

4.5 Conclusions

Subsistence farmers in the Azuero region of Panama continue to crop "traditional" varieties containing substantial amounts of phenotypic diversity. The naming practices of farmers partially coincide with classifications based on a broad suite of traits, and correlation is stronger for rice than for maize. Farmers have adopted "modern" maize and rice varieties. Furthermore, farmers' classification of populations as "modern" and "traditional" types is substantiated by phenotypic differences. Many rice populations are heterogeneous, but farmers recognize this as being due to admixture where seed traits are concerned. Over the small distances represented in the study, there does not appear to be a correlation between genetic and geographical distance. The farmers in this study retain a significant amount of maize and rice diversity and their management is very dynamic where incorporating "modern" germplasm and tolerating admixture is concerned. Continued collection and characterization of these materials will be required if plant breeding programs are to capitalize on this constantly-evolving diversity.

4.6 Tables

Table 4.1 Means and ranges for selected maize and upland rice traits and least-squared means for traits that differed between "modern" and "traditional" populations collected from farmers in Panama, 2005.

Trait	Units	Mean	Range	Least-squares means		Sig.
				Traditional	Modern	
Maize						
Plant height	cm	312	223 - 366			
Ear height	cm	152	100-194			
Ear to plant height ratio	ratio	0.49	0.37 - 0.62	0.5	0.46	**
Leaf width	cm	6.8	5 - 7.6	6.6	6.9	**
Leaf length	cm	100	85 - 119	98.8	103.8	**
Leaves above the ear	count	9.2	7.7 - 10.5			
Tassel length	cm	38.6	30.7 - 46.6			
Secondary tassel branches	count	5.2	1.9 - 10.3	5.5	4.7	*
Row number	count	12.8	11.1 - 14.9			
Ear number	count	1.1	0.7 - 1.7			
Ear length	cm	15.6	11.5 - 18.2			
Ear diameter	cm	3.8	2.2 - 4.6	3.6	4	**
Cob diameter	cm	2.0	1.2 - 2.7	1.9	2.1	**
Cob rachis diameter	cm	1.7	1.1 - 2.3	1.6	1.8	**
Grains per row	count	27.3	20 - 35.3			
Grain depth	cm	0.98	0.71 - 1.29	0.94	1	*
Grain width	cm	0.85	0.63 - 0.99	0.81	0.86	**
Grain thickness	cm	0.42	0.35 - 0.57			
Days to silking	days	60.2	55 - 67	60.7	59.5	*
Days to tasselling	days	55.2	52 - 64			
Days to senescence	days	108.6	103 - 116			
Husk weight	g husk^{-1}	31.8	12.5 - 50.6			
Cob weight	g cob^{-1}	14.5	5.1 - 29.1	12.4	16.6	**
100-grain weight	g	20.3	10.4 - 25.5	18.8	22	**
Ear yield	g ear^{-1}	79.5	46 - 139.3	75.1	87.6	*
Field yield	Kg ha^{-1}	3715	1957 - 6128			
Rice						
Culm length	cm	134.2	99 - 173.2			
Leaf width	cm	2.2	1.7 - 2.8	68.6	63.3	**
Leaf length	cm	67.2	52.4 - 79.2	2.1	2.24	**
Panicle length	cm	28.7	19.4 - 39	29.5	26.2	**
100-grain weight	g	2.5	1.8 - 3.1	2.43	2.6	**
Days to flowering	days	96.9	71 - 125	98.7	91.8	**
Days to maturity	days	125.0	94 - 132			
Field yield	Kg ha^{-1}	1956	430 - 3791	1788	2471	**

Table 4.2 The percent of maize and upland rice populations exhibiting presence of selected nominal traits measured in an agromorphological trial in Panama, 2005.

Trait	Trait values (% of populations exhibiting presence of a given trait value)
Maize	
Stalk color	Green (100%), Sun red (92%), Purple (42%), Brown (13%)
Node color	Green (100%), Sun red (94%), Purple (44%), Brown (8%)
Row shape	Regular (98%), Spiral (73%), Irregular (65%), Straight (33%)
Ear shape	Cylindrical-Conical (98%), Conical (83%), Cylindrical (77%), Round (2%)
Kernel shape	Level (100%), Rounded (75%), Dented (71%), Pointed (4%), Shrunken (2%)
Kernel color	Yellow (100%), White (42%), Orange (21%), Purple (15%), Mottled (2%)
Pubescence	Sparse pubescence (100%)
Tillering	No tillering (100%)
Rice	
Leaf pubescence	Glabrous (66%), Intermediate (47%), Pubescent (7%)
Basal leaf color	Green (79%), Purple (32%)
Collar color	Light green (100%), Green (6%), Purple (2%)
Auricle color	Pale green (94%), Purple (6%)
Node color	Green (72%), Purple (17%), Light gold (13%), Light purple (2%)
Internode color	Green (74%), Purple (17%), Light gold (13%)
Panicle branching	Heavy (89%), Light (9%), Clustering (2%)
Awns	Short partly awned (75%), Short fully awned (50%), Absent (32%), Long fully awned (2%), Long partly awned (2%)
Awn color	Straw (68%), Black (13%), Red (6%), Purple (4%)
Early apiculus color	Straw (70%), Black (21%), White (8%), Brown (8%), Red apex (8%), Purple apex (6%), Red (4%)
Stigma color	White (77%), Purple (23%), Light purple (13%), Yellow (4%)
Sterile lemma color	Straw (55%), Gold (27%), Red (11%), White (8%), Purple (6%)
Hull color	Straw (57%), Brown (34%), White (13%), Purple spots (13%), Purple (2%)
Hull pubescence	Glabrous (70%), Short hairs (53%)
Seed coat color	White (100%), Red (2%)
Ligule type	2-cleft (100%)
Ligule color	Whitish (100%)

4.7 Figures

Figure 4.1 Flow chart outline of the laboratory proceedure used for genotyping based on bulked maize DNA.

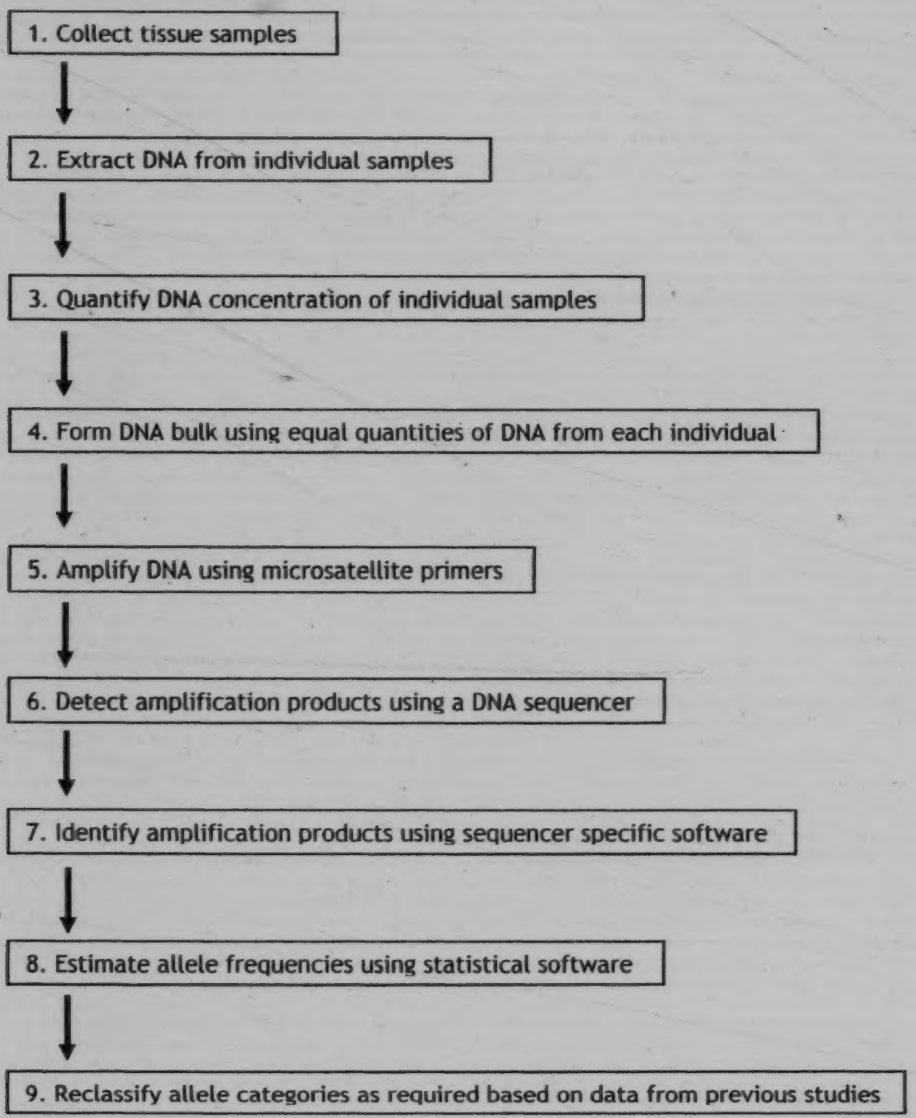
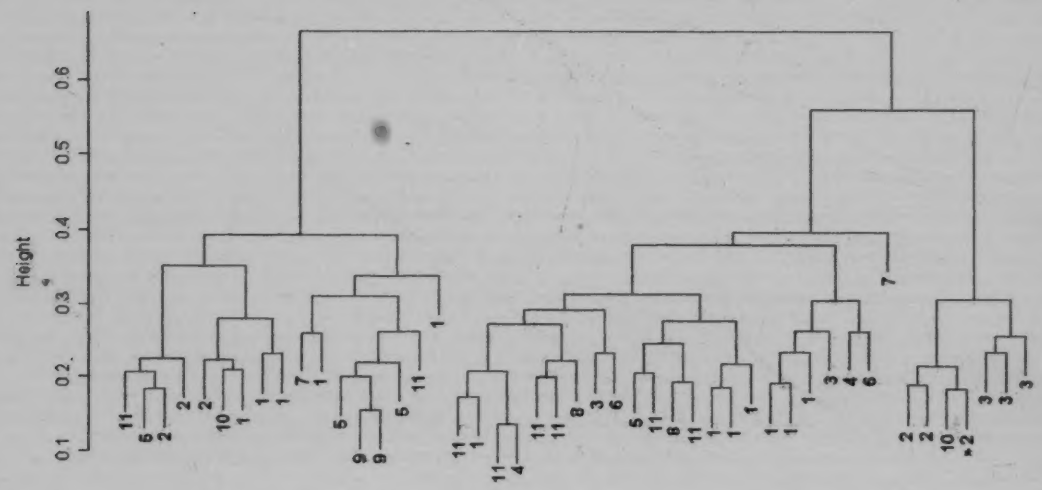

1. Collect tissue samples
2. Extract DNA from individual samples
3. Quantify DNA concentration of individual samples
4. Form DNA bulk using equal quantities of DNA from each individual
5. Amplify DNA using microsatellite primers
6. Detect amplification products using a DNA sequencer
7. Identify amplification products using sequencer specific software
8. Estimate allele frequencies using statistical software
9. Reclassify allele categories as required based on data from previous studies

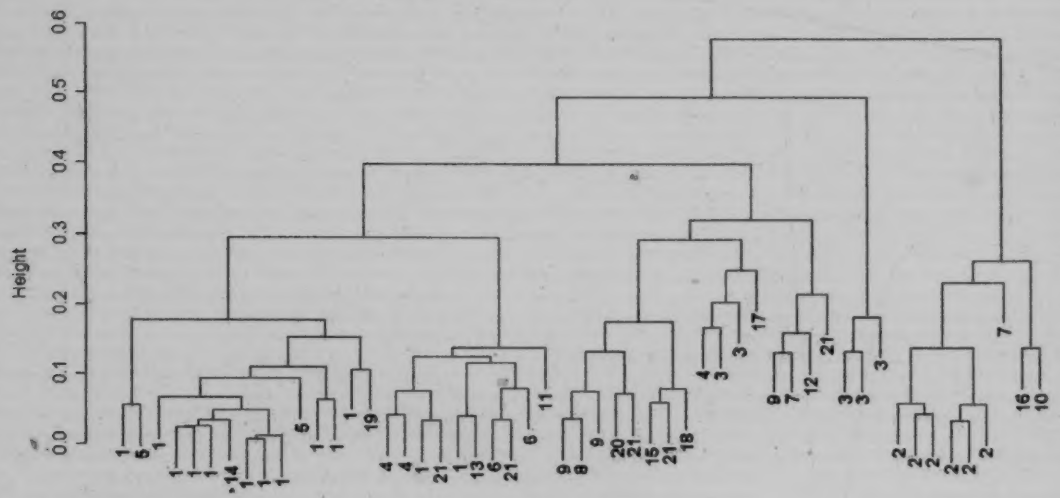
Figure 4.2 Cluster dendrogram (Gower's distance, Ward's method, phenotypic and molecular data) of maize populations collected from farmers in Panama, 2005.



Farmer-named varieties: 1 = Isleño, 2 = Guararé, 3 = Blanco, 4 = Maíz Perro, 5 = Amarillo, 6 = Colorado, 7 = Palomita, 8 = Tableño, 9 = Capullo Morado, 10 = Tusi morado, 11 = No name

*** indicates check variety**

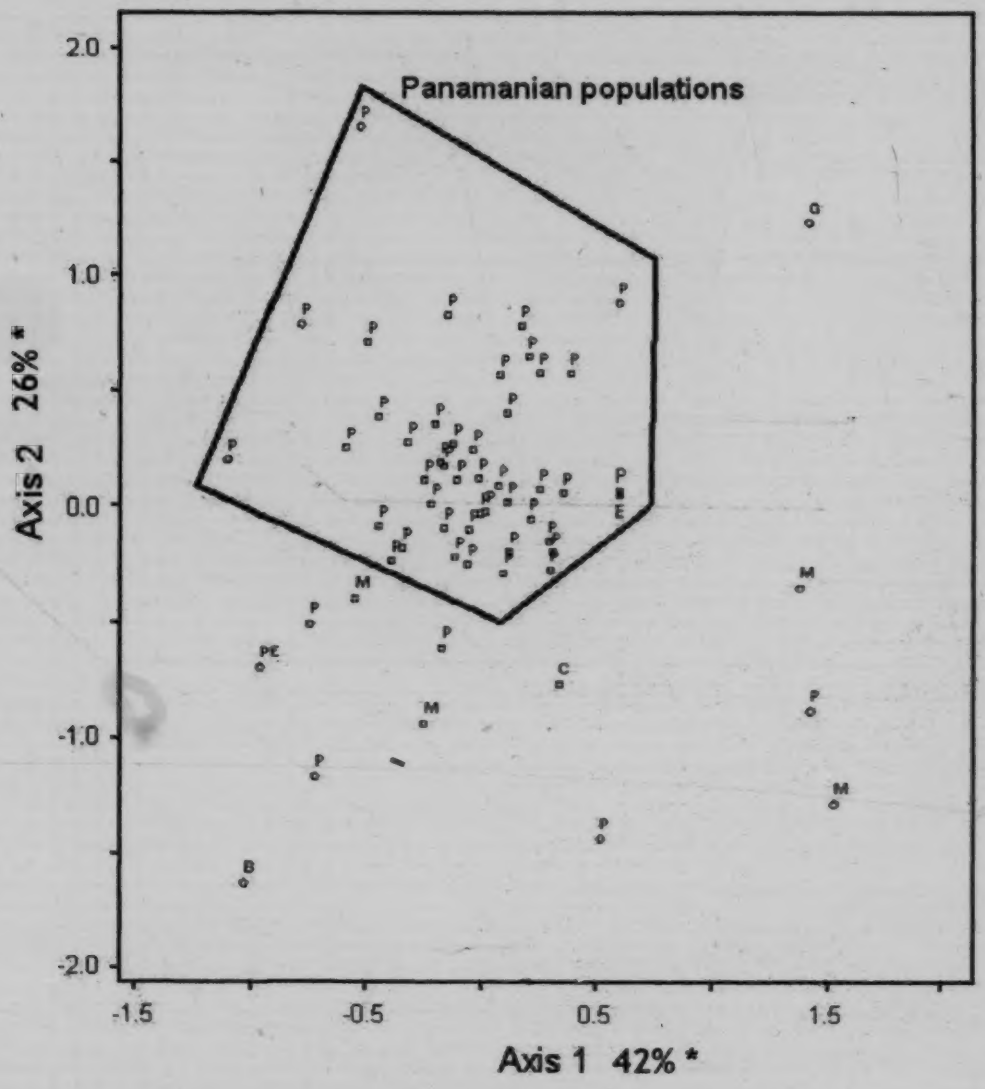
Figure 4.3 Cluster dendrogram (Gower's distance, Ward's method, phenotypic data) upland rice populations collected from farmers in Panama, 2005.



Farmer-named varieties: 1 = Lubón, 2 = Culí Moreno, 3 = Lijero, 4 = Chino Blanco, 5 = Tío Fulo, 6 = Guayaquil, 7 = Coría, 8 = Colombia, 9 = Cañacilla, 10 = Zaíno, 11 = Raízoro, 12 = Plata, 13 = Pajareño, 14 = Orisíca, 15 = Darién, 16 = Chombo, 17 = Chino Morado, 18= Caballón, 19 = Bonita, 20 = Amarillo Pedregal, 21 = No name

*** indicates check variety**

Figure 4.4 Ordination (Euclidean distance, Non-metric multi-dimensional scaling, molecular data) of maize populations collected in Panama in 2005 and populations collected elsewhere in Latin America (B = Bolivia (n = 1), C = Cuba (n = 1), E = Ecuador (n = 1), G = Guatemala (n = 1), M= Mexico (n = 4), P = Panama (n = 49), PE = Peru (n = 1)).



* = amount of variation explained by each axis

5.0 Maize and upland rice traits of importance for farmers practicing manual rainfed agriculture in the humid tropics: a Panamanian case-study[13]

5.1 Abstract

The agronomic practices and concerns of resource-poor farmers in comparable ecozones are often similar across countries and regions. Crop ideotypes have helped guide selection for yield under high fertility monoculture conditions in formal breeding programs and could be used to direct breeding for the agricultural conditions of resource-poor farmers. However, the objectives and selection criteria of subsistence farmers may differ from those of formal breeding programs. This study illustrates a simple survey method for detecting crop traits that are important to farmers, and describes results for upland rice and maize ideotypes cropped by subsistence farmers in Panama. Our results suggest formal breeding programs are working on individual crop traits of importance to resource-poor farmers, but they may not be developing varieties that have multiple individual traits (ideotypes), which farmers desire. National breeding programs should play a crucial role in identifying and breeding for regional ideotypes that vary with farming practices and cultural preferences. The field survey techniques reported herein are easily repeatable, quickly orient plant breeders towards crop traits that are potentially important to farmers, provide information on the processes underpinning trait importance, and capitalize on decades of farmer experience.

[13] This chapter as developed by B. Love, M. Luckert, and D. Spaner has been submitted to *Euphytica*.

5.2 Introduction

Participatory breeding programs can help link plant breeding programs more tightly to resource-poor farmers' needs (Sperling et al., 2001). Resource-poor farmers are farmers whose resources do not permit a secure livelihood (Chambers and Ghildyal, 1985). Conducting plant breeding for this group is important because, globally, 450 million resource-poor farmers support 1.25 billion people (Mazoyer, 2001). Many resource-poor farmers practice swidden agriculture (rotating fields between long fallows and short cropping cycles by slashing and burning the biomass that accumulates during fallow periods) (Crutzen and Andreae, 1990), but participatory breeding for swidden agriculture has only recently been researched intensively in Central America (Trouche, 2005). These farmers often practice subsistence agriculture (consuming most of their agricultural production with only small surpluses being sold to market). Identifying crop ideotypes for resource-poor farmers is a first step towards breeding varieties that meet these farmers' needs (Ceccarelli, 1996).

Ideotype breeding is well developed where high-fertility environments (Donald, 1968; Mock and Pearce, 1975; Peng et al., 1999) and consumer preferences for commercial crops (Van Lieshout, 1993) are concerned. Techniques for identifying ideotypes for resource-poor farmers are not as well defined. Subsistence farmers' continued cropping of "traditional" rather than "improved" varieties suggests more extensive ideotype research for poor farmers is required. Although farmer visual evaluation of varieties is now a common means of obtaining information about trait importance (Sperling et al., 2001) such evaluation is usually done by small groups of farmers appraising a handful of unfamiliar improved varieties at a research station (e.g.

Abeyasekera et al., 2002). Recently, field survey techniques have been used to identify traits of importance to farmers (Bellon et al., 2005), but the focus has been on a predetermined list of traits, which potentially limits farmers' responses.

Maize is Latin America's most important grain crop (28 million ha), while upland rice accounts for forty percent of rice production in Latin America and the Caribbean, and covers 4.6 million ha (FAO, 2001b). Our study was conducted in Panama where rice (*Oryza sativa* L.) and maize (*Zea mays* L.) are the primary staple grain crops (McKay, 1990) and swidden agriculture is common (Fischer and Vasseur, 2000). The present study targeted subsistence farmers in Panama and had the following objectives:

1. To implement a simple field survey method for identifying crop traits of importance to subsistence farmers.
2. To empirically assess the importance of maize and upland rice traits.
3. To compare and contrast important traits with formal breeding program objectives.

5.3 Methods

5.3.1 Study area

The study was conducted in the uplands of Herrera province in the Azuero region of the Republic of Panama in December 2004 (Figure 5.1). Panama is situated in tropical Central America (7°- 9° N and 77° - 83° W), and Herrera province is considered to be the agricultural heartland of the country (Jaen-Suarez, 1978). The upland zone where the study was conducted lies between 600 - 1000 m.a.s.l, is comprised of steep broken hills,

and includes Holdridge's (1967) tropical moist, premontane wet, and tropical wet forest life zones.

5.3.2 Farmer selection and interview procedures

Access difficulties (poor road infrastructure, lack of telecommunication technology, respondents' highly variable work schedules) required the use of a targeted small-sample survey. Census data (Contraloría, 2001b) and consultation with local agricultural extensionists was used to create a sampling frame of towns in the upland zone. The sampling frame consisted of towns with more than 5 houses and that were accessible by 4 x 4 vehicles and/or within three hours walking distance of the nearest vehicularly accessible drop-off point. Towns were then stratified into those belonging to areas practicing swidden agriculture, and areas in transition to permanent agriculture. Five towns were selected at random from each stratum (Figure 5.1). Public meetings were held in selected towns to outline the research process (including participants' rights) and to recruit farmer participants (Appendix 5.1). Farmers' participation in meetings and the study was voluntary.

The study employed a semi-structured interview administered at the respondents' homes. Interviews (Appendix 5.2) lasted up to 45 minutes and consisted of two general categories of questions: 1) farmer information (e.g. age, education, land use) and 2) open-ended questions regarding maize and rice traits (listing of positive and negative traits and discussion of the rationale for their importance). Two approaches were used to gather information about maize and rice traits of importance:

1. Farmers, based on their experience, were asked to list the positive and negative traits of the populations of maize and rice they currently cropped.
2. Farmers were asked to list traits they would desire in a new maize or rice variety.

Listing of positive and negative traits for currently cropped populations was conducted prior to listing desirable traits for new varieties.

In the present study, the terms population and variety are defined as follows:

Population: A group of genetically related plants of a particular crop species, which is managed under the same regime (e.g. farmer X's yellow maize).

Variety: A distinct subunit of a crop species that has been defined by plant breeders. The concept of variety is restricted to the products of formal breeding programs, but populations may belong either to varieties or "unimproved" materials managed by farmers.

5.3.3 Analyses procedures

Crop traits reported by farmers were assigned to one of seven categories (yield traits, consumption qualities, processing qualities, grain traits, plant traits, stress related traits, and management traits). Percentages were used to illustrate the predominance of specific traits (e.g. Bellon et al., 1998). The percent of farmers reporting a trait at least once and the percent of crop populations reported to have the trait were used to assess farmer preference for a trait and trait prevalence among populations, respectively. Analysis of farmer responses was done separately for existing populations and new

varieties. Trait importance was assessed based on: trait preference and prevalence based on existing populations and trait preference in new varieties.

5.4 Results

5.4.1 Sample characteristics

A total of 68 farmers (67 males) who managed separate farms were interviewed. Farmer age ranged from 24 to 80 (mean = 49). Level of formal education ranged from 0-9 years of schooling (mean = 3.9) and 75 percent of farmers were native to their communities (i.e. born there). Selected towns had a combined total adult population (> 18 years of age) of 528 with the number of adults per town ranging from 15 – 115 (mean = 53) (Contraloría, 2001b).

5.4.2 Crop traits

Often, reciprocal positive and negative traits (e.g. drought tolerance = positive, drought susceptibility = negative) indicated a single trait. Reciprocal trait pairs were combined into a single trait when calculating preference percentages. The percent of populations with the positive or negative version of the trait provided an indication of trait availability. Cases where the negative variant of a trait had high prevalence relative to the positive variant indicated a potential trait availability deficiency. In some cases a trait potentially conflicted with another trait (e.g. preference for both tall plants and lodging resistance) indicating cases where potential trade-offs exist between traits.

When farmers report on what they desire in new varieties they are free to mention traits that are not available in their crop populations and can emphasize traits of

importance when considering adoption. Defining a short-list of important traits (Table 5.3), while based on empirical evidence, also requires subjective judgment. In the present study, maize traits reported by at least 15% of farmers and rice traits reported by at least 20% of farmers were deemed to be important (see Table 5.1). Traits falling below these thresholds were considered to be important in cases where an availability deficiency (see Table 5.1) or a preference in new varieties was evident (Table 5.2). Availability deficiencies are interesting because they indicate a situation where supply is not meeting demand and breeding, including introduction of the desired trait from foreign germplasm, could lead to substantial improvement. However, addressing availability deficiencies while ignoring other important traits would be inappropriate because any new variety must have a competitive trait profile compared to those of currently grown crop populations. Traits farmers desire in new varieties may be of special importance because their presence may make or break adoption.

5.4.3 Upland rice

Of the 68 respondents 50 reported growing rice and provided information on a total of 87 rice populations with each farmer reporting on 1 to 4 populations (mean =1.7). Farmers reported 34 upland rice traits of interest, but only 21 traits were mentioned by at least 10% of farmers (Table 5.1). The percent of rice populations with positive and negative variants of a trait tended to be high and low, respectively, with a few exceptions (Table 5.1). Farmers reported 26 different traits to be desirable in new varieties, but only 8 traits were mentioned by at least 10% of farmers (Table 5.2). No new traits (i.e. traits not reported by farmers for existing populations) were reported when listing desirable

traits for new varieties. Based on this information 16 important upland rice traits were identified (Table 5.3).

5.4.4 Maize

Fifty-seven farmers offered information on 75 maize populations with the number of populations per farmer ranging from 1 to 4 (mean = 1.3). Farmers reported 29 maize traits of interest, but only 13 traits were mentioned by 10% or more of farmers (Table 5.1). Farmers reported 25 different traits to be desirable in new varieties, but only 6 traits were mentioned by at least ten percent of farmers (Table 5.2). No new traits (i.e. traits not reported for existing populations) were mentioned for new varieties. However, drought tolerance was a desired trait for new varieties despite not being mentioned by more than 10% of farmers for existing populations. Based on this evidence 11 important maize traits were identified (Table 5.3).

5.5 Discussion

Traits found to be important in this study were searched for in the plant breeding literature to determine whether they were being studied. The literature search queried major databases (e.g. CAB Abstracts, AGRICOLA, Patent Registries) and journals publishing on international plant breeding (e.g. Emphatic, Crop Science).

5.5.1 Traits of importance to subsistence farmers

5.5.1.1 Rice

In the present study the important traits constituting an upland rice ideotype (Table 5.3) were: yield, good panicles (long with many grains), good grain-fill, good-to-eat (soft non-gummy texture), easy threshing and de-hulling, glabrous hulls, earliness, high-tillering capacity, resistance to lodging, pests, shattering, and false smut (*Ustilaginoidea virens* Cooke), and tolerance to drought and infertile soils. Farmers noted a disadvantage of earliness is increased bird damage, but long awns (> 5cm) and dark hulls can deter birds. With regards to lodging resistance farmers in this study harvest rice by hand and tall rice (95 – 115 cm) is required for ergonomic reasons (i.e. prevent stooping) and makes lodging resistance based on semi-dwarf stature unacceptable. Good grain-fill, lodging resistance, and drought resistance were preferred traits for both existing populations and new varieties. These traits also had evident availability deficiencies and should receive special attention. Shattering and panicle rot resistance were included as important traits on the basis of availability deficiencies.

While some of these traits' importance is clear (e.g. pest resistance) the importance of other traits is not. Understanding the processes underlying the importance of these traits is useful when considering their broader applicability. Subsistence farmers manually process grains and rice populations that are difficult to thresh or de-hull require more manual labor during processing. However, the importance of easy processing may be temporally unstable because technological change could reduce its importance in the future. An additional problem with easy threshing is a potential trade-off with shattering resistance. This is because rice populations that are resistant to shattering are difficult to

thresh. Pubescent hulls are disliked because they cause irritation during processing, are believed to be associated with fungal rots, and are difficult to sow in rainy conditions. High-tillering capacity is valued because it helps compensate for poor germination or low seeding density.

Most of the above traits have been researched in the plant breeding literature. High-yield, long panicles with many grains, and good grain fill are being bred for in rice (Peng et al., 1999). Subsistence rice farmers are known to have exacting quality preferences (Virk et al., 2003). Earliness (Fisher et al., 2001) and lodging resistance based on characteristics other than height (Hai et al., 2005) are important in cereal breeding. Awns (Bullard, 1988) and dark colored grains (Subramanian et al., 1983) are used to deter birds. Drought resistance and performance in infertile soil are major upland rice breeding objectives (Arraudeau, 1995). Improved disease resistance and pest resistance (Bonaman et al., 1992), including false-smut (Biswas, 2001), are central rice breeding objectives. High-tillering capacity is an important characteristic of upland rice (Dingkuhn et al., 1999) and glabrous hulls are preferred by rice breeders (Khush et al., 2001). Based on our review of the literature only easy threshing and dehulling do not appear to have been studied extensively.

5.5.1.2 Maize

In the present study the important traits making up a maize ideotype (Table 5.3) were: yield, good ears (long with many kernels), weevil (*Sitophilus zeamais* Motschulsky), ear rot, and lodging resistance, fertilizer responsiveness, small kernels, high test-weight, easy-shelling and tolerance to drought and infertile soils. With the

exception of drought tolerance, all traits reported by farmers as being preferred in new varieties were also reported as preferred traits by at least 15% of farmers for existing maize populations (Table 5.3). Weevil and ear rot resistance as well as drought tolerance should receive special attention because they were preferred in new varieties, but had notable availability deficiencies.

These traits are important to farmers for a number of reasons. Weevil resistance was preferred because maize is stored in open bins without chemical protection and storage losses due to weevils are a problem. Ear rot resistance was preferred because the first maize crop is harvested under rainy conditions that favor fungal disease. Farmers believe thick husks, which tightly cover the end of the cob, prevent weevil and fungal damage. Preference for fertilizer responsiveness is an indication subsistence farmers, including swidden agriculturalists, are using chemical fertilizers. Small kernels were important because they reduce labor requirements when feeding baby-chicks because milling is not required. Easy shelling is currently important because maize is hand shelled, daily, for feed and food and easy shelling reduces labor requirements. However, mechanical shellers could reduce the future importance of this trait.

The plant breeding literature has addressed many of the above traits. Yield is a fundamental maize breeding objective but selection has increased kernel weight (larger size) rather than quantity (Duvick, 2005). Weevil (Derera et al., 2001) and ear rot (Silva et al., 2007) resistance are being bred for, and selection for robust husk cover is known to prevent insect and fungal damage (Warfield and Davis, 1996). Tolerance to drought and low soil fertility (Duvick, 2005) are priorities within maize breeding. Fertilizer responsiveness and lodging-resistance are major breeding program objectives (Khush,

2001) and test-weight advantages are commonly selected for in maize (e.g. Kramer, 2007). To our knowledge, only small kernel size and easy shelling have not been reported on extensively in the plant breeding literature.

5.5.2 Comparing maize and rice

Many of the same categories and traits are important for both maize and rice. In particular yield, plant traits, and stress related traits figured prominently for both maize and rice based on a large number of highly preferred traits being mentioned for these categories. Common traits preferred across both maize and rice included: yield, easy shelling/threshing, lodging resistance, earliness, pest and rot resistance, tolerance to drought and infertile soils, and fertilizer responsiveness. It is interesting to note drought tolerance and resistance to rots are simultaneous concerns in the humid tropics. These traits may be important for other crops farmed under similar conditions.

5.5.3 Future considerations for survey methods

Farmers did not report traits for new varieties other than those reported for existing populations. This may be because prior discussion of traits in existing populations focused farmers' attention on these traits, but may also result from farmers finding it difficult to value traits they have not experienced first hand. This limitation could be addressed by varying the order of questioning from farmer to farmer and by having farmers report on a list of traits they may not be aware of. Conversely, farmers may not report important traits that are taken for granted. For instance, without radical changes to harvesting techniques it is unlikely farmers would accept plants of semi-dwarf

stature. Thus, tall stature is important to all farmers, but only 10% of farmers reported it to be a positive trait because it is taken for granted (an assumed trait).

For best results these survey techniques should be applied and analyzed by someone with plant breeding knowledge so that reciprocal, trade-off, and assumed traits can be identified. The empirical data these techniques produce must be subjectively interpreted to define a suite of "important" traits (ideotype). If the relative importance of traits is of interest, more complex survey and analysis techniques permitting evaluation of limited dependent choice models (Maddala, 1983) may be appropriate.

5.5.4 Crop ideotypes

The results of the present study suggest, with the possible exception of processing qualities, formal breeding programs are largely aware of maize and upland rice traits of importance to swidden agriculturalists in the humid tropics. This congruence does not necessarily mean varieties having farmer-desired trait profiles (ideotypes) are being developed. The suites of important traits reported for maize and upland rice in Table 5.3 constitute ideotypes that should be considered when breeding maize and upland rice for subsistence farmers in Panama. These ideotypes may be important elsewhere in the humid tropics. The potential broader applicability of our results is evidenced by their agreement with a study in southern Mexico which found: easy shelling, lodging resistance, drought tolerance, ear rot resistance, and pest resistance to be very important for resource-poor farmers growing maize (Bellon et al., 2005).

5.6 Conclusions

Farmers have a sophisticated understanding of the traits they desire in crop varieties. Farmer reporting on these traits can help construct ideotypes, but this approach may be limited only to traits farmers are familiar with. Moreover, some traits may vary in importance because of changing or variable circumstances. National breeding programs should take the lead in applying these survey tools, to identify ideotypes, where contextual variability (e.g. cultural taste preferences, manual processing practices, livestock preferences) and limited farmer experience with novel traits influence trait importance.

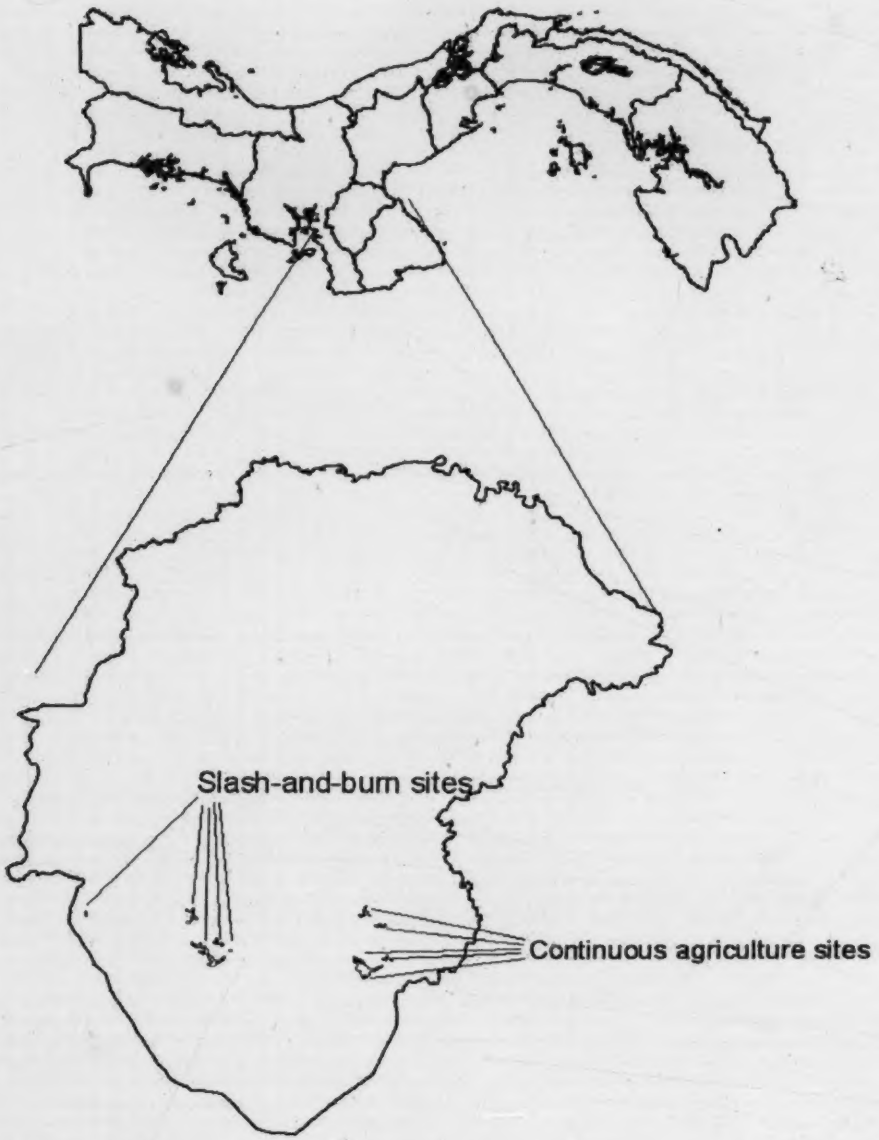
Plant breeding is a broad field and many traits have been reported on in the literature. Formal breeding programs are researching individual traits of importance to farmers in this study. However, it is unclear if study of individual traits has resulted in the packaging of combinations of traits into ideotypes subsistence maize and upland rice farmers are willing to adopt. This study outlines maize and upland rice ideotypes for subsistence farmers in Panama that may be applicable elsewhere in the humid tropics. Moreover, it demonstrates farmer assessment of currently cultivated populations can be used to uncover ideotypes.

These field survey techniques have limitations. Traits that are unfamiliar to farmers may not be detected and traits of fundamental importance may not be reported because they are considered common knowledge. Furthermore, knowledge of plant breeding is helpful when interpreting results because of the need to identify reciprocal traits and trade-offs. Even with expert guidance the interpretation of these data is subjective and does not provide information on the relative importance of traits. Despite

these limitations these low-cost techniques are easily repeatable and may be preferable to farmer evaluation of on-station variety trials. This is because these survey techniques quickly orient plant breeders towards farmers' preferences, provide information on the processes underpinning trait importance, and capitalize on decades of farmer experience.

5.7 Figures

Figure 5.1 Study site towns in Herrera province, Panama



5.8 Tables

Table 5.1 Traits belonging to specific categories reported by at least 10% of farmers (%F) for maize and upland rice populations cropped in 2004 in the humid tropics of Panama. The percent of populations with the positive (%Pos) and negative (%Neg) variants of the trait are given

RICE TRAITS	%F	%Pos	%Neg	MAIZE TRAITS	%F	%Pos	%Neg
YIELD							
Good panicle	42	30	2	Good ear	30	23	1
Good grain fill	38	16	16	Good yield	30	21	3
Yield	30	20	1				
CONSUMPTION QUALITIES							
Good-to-eat	42	26	1	Marketable	14	9	1
Grain expansion	18	14		Good taste	11	8	
PROCESSING QUALITIES							
Easy to thresh	34	21	3	Easy to shell	18	13	3
Easy to hull	30	21					
Shatter resistant	16	3	7				
Dries quickly	12	7					
GRAIN TRAITS							
Dense grain	12	16		Small kernels	26	20	2
				High test-weight	21	13	4
PLANT TRAITS							
Earliness	40	24	2	Resists lodging	19	12	4
Tillering capacity	24	14		Earliness	12	8	1
Resists lodging	20	3	13				
Glabrous hulls	18	6	6				
Tallness	10	6					
STRESS ADAPTATION							
Infertile soil tolerance	30	18	7	Weevil resistance	58	40	15
Resists false smut	26	2	15	Ear rot resistance	44	23	12
Resists drought	20	9	6	Infertile soil tolerance	19	13	1
Resists pests	20	6	6				
Resists panicle rots	16	5	9				
MANAGEMENT							
Herbicide tolerant	14	6	2	Fertilizer responsive	28	12	11
Fertilizer responsive	12	5					

Table 5.2 Maize and upland rice traits that at least 10% of farmers (%F) reported to be desirable in new varieties, Panama, 2004.

Rice traits	%F	Maize traits	%F
Drought tolerance	29	Yield	33
Yield	26	Weevil resistance	28
Good-panicle	21	Ear rot resistance	23
Lodging resistance	19	Good ear	21
Good-to-eat	19	Drought tolerance	16
Good-grain-fill	10	Lodging resistance	14
Infertile soil tolerance	10		
Easy to thresh	10		

Table 5.3 Important traits reported by farmers for maize and upland rice based on trait preference and desirability in new varieties Panama, 2004

Crop trait	Category	Trait preference (Table1. %F)	Population deficiency (Table 1. %Ppos, %Pneg)	Desirable in new varieties (Table 2. %F)
RICE				
Good panicle	Yield	X		X
Overall yield	Yield	X		X
Good grain-fill	Yield	X	X	X
Earliness	Plant trait	X		
Tillering capacity	Plant trait	X		
Lodging resistance	Plant trait	X	X	X
Glabrous hulls	Plant trait		X	
Easy to thresh	Processing	X		X
Easy to dehull	Processing	X		
Shatter resistant	Processing		X	
Good-to-eat	Consumption	X		X
Infertile soil tolerance	Stress	X		X
False smut resistance	Stress	X	X	
Pest resistance	Stress	X	X	
Drought tolerance	Stress	X	X	X
Panicle rot resistance	Stress		X	
MAIZE				
Overall yield	Yield	X		X
Good ear	Yield	X		X
Small kernels	Grain trait	X		
High test-weight	Grain trait	X		
Lodging resistance	Plant trait	X		X
Easy to shell	Processing	X		
Weevil resistance	Stress	X	X	X
Ear rot resistance	Stress	X	X	X
Infertile soil tolerance	Stress	X		
Drought tolerance	Stress		X	X
Fertilizer responsiveness	Management	X	X	

6.0 Evaluation of the initial performance of four native timber species under on-farm and on-station trial conditions in Panama

6.1 Abstract

Reforestation with native tree species is increasing in importance. On-farm trials may be required to provide credible performance estimates for landowners interested in pursuing reforestation through plantation agroforestry. This paper describes a two-year (2004 and 2005), multi-location (low and medium rainfall) on-farm trial in Panama, which evaluated the growth of four native timber species: *Cedrela odorata* L. (Cedro Amargo), *Samanea saman* (Jacq.) Merr. (Guachapalí), *Pachira quinata* (Jacq.) W.S. Alverson (Cedro Espino), *Tabebuia rosea* (Bertol.) A. DC. (Roble). The on-farm trial grew out of, and is compared to, an on-station multi-location trial, established in 2003, which tested a larger suite of species at the same locations. *C. odorata* consistently performed poorly both on-farm and on-station with low average survival and monthly growth rates. Compared to on-station trials, the on-farm trials did not detect a location effect and yielded lower survival and growth rate estimates. The ratio of blocking to residual error variance was higher in the on-farm than the on-station trial suggesting blocking captured variation more effectively in the on-farm trial. The importance of micro-site environment was exemplified by a negative correlation between tree performance and the slope gradient of individual plots in the on-farm trial. The practical lessons learned during the establishment of the on-farm timber species trial paralleled experiences with on-farm trials for annual crops. The results of this study indicate on-

farm trials are potentially an important tool for developing recommendations for plantation forestry.

6.2 Introduction

Plantation forestry is an increasingly important aspect of reforestation. However, most species used in plantation reforestation are exotics (Evans, 1999). Exotic tree species have been shown to replace native tree species through invasion (Yamashita et al., 2003) and this may negatively impact biodiversity (Richardson, 1998). Despite growing interest in the use of native tree species for reforestation (Butterfield and Espinoza C, 1995; Hooper et al., 2002; Montagnini et al., 2003), lack of silvicultural information remains a major limitation to the use of native species in regions such as Panama (Condit et al., 1993).

On-station trials are experiments (e.g. variety trials) that are set up and managed by researchers at a research station. Traditionally, on-station trials have been used to generate recommendations for landowners farming in similar agroecological zones (Gomez and Gomez, 1984). However, research station conditions in developing countries may differ greatly from those of landowners and on-farm research (experiments conducted in farmers' fields with varying levels of farmer participation) is often required to produce credible recommendations (Parkhurst and Francis, 1986). On-farm agroforestry trials (e.g. Carpenter et al., 2004; Kanmegne and Degrande, 2002; Kidanu et al., 2005; Nyadzi et al., 2003) are relatively new and are regarded as difficult to design, implement, and evaluate (Scherr, 1991). Moreover, practical information about on-farm agroforestry trials' strengths and weaknesses is needed (Pinney, 1991). The objectives of this study were to: 1) assess the initial performance of four native timber species at two

locations in Panama for use in plantation forestry, and 2) compare tree species recommendations derived from standard on-station trials with those obtained from landowner managed on-farm trials.

6.3 Materials and methods

6.3.1 Study site

Panama is a small, tropical, Central American country situated at 7° - 9° N and 77° - 83° W (CNRFP, 1995). On-station and on-farm trials were established in the Río Hato district of Cócle province and the Pedasí and Tonosí districts of Los Santos province (Figure 6.1). Both locations are coastal with trial sites not exceeding altitudes of 200 m.a.s.l. The Rio Hato location is relatively dry with an average annual rainfall of 1107mm and 6.7 dry months (Wishnie et al., 2007). This location includes Holridge's (1967) tropical dry and premontane moist forest life zones. In contrast, the Los Santos location contains tropical moist and premontane humid forest life zones, and is wetter receiving an average annual rainfall of 1946mm with only 5.2 dry months (Wishnie et al., 2007). Agricultural soil capacity is non-arable to arable with severe limitations in Río Hato, and arable with few to severe limitations in Tonosí and Pedasí (IGNTG, 1988). Site observations indicated that steep slopes were the main site characteristic limiting performance in Los Santos while steep slopes, severe erosion, sandy soils, and hardpans were the main limitations in Río Hato.

6.3.2 On-farm trial design

A total of 26 trial sites belonging to 24 landowners were established over the 2004 and 2005 seasons. One to four timber tree species (*C. odorata, P. quinata, S. saman, T. rosea*) were planted at each site in mono-specific plantation plots of ~100 trees. Thirteen sites were established in each of the two years with a final total of 16 sites in Los Santos and 10 sites in Rio Hato. Consistent with the on-farm nature of the trial, landowners' preferences influenced the number, species identity, size, and shape of the plots established at each site. The resulting design was considered an unbalanced incomplete block design. In total 16 *C. odorata*, 17 *T. rosea*, 20 *P. quinata*, and 21 *S. saman* plantation plots were established. Forty-three plots were established in Los Santos and 31 in Rio Hato, and all species were present on at least 6 sites at each location.

Plots were delineated prior to planting and species were randomly assigned to the plots. Landowner and site selection was non-random, with referrals from local researchers, civil servants, and ombudspersons used to identify landowner collaborators. Landowner collaboration was entirely voluntary and participants identified sites upon which plantation plots could be established. These sites tended to be adjacent to fencing, in a corner of the property, and often on steeper than average terrain. Plots used 3m × 3m spacing except in three cases in Los Santos where 6m × 6m spacing was used.

In 2004 planting occurred between 12 July and 5 August at Rio Hato and 25 June and 1 July at Los Santos. In 2005 planting occurred between 13 July and 20 July at Rio Hato and 26 June and 3 July at Los Santos. Seedlings for planting were produced in a nursery three months prior to planting, in trays, using soil plugs (low-nutrient mix: sand, rice hulls, and black soil). This ensured uniformity and that seedlings were of the highest

possible standard for each species. Sub-plots were delineated within plots by randomly selecting a starting tree, and subsequently defining a sub-plot of ~60 trees that was as rectangular as possible using a random direction from the origin. During measurement all trees within sub-plots were evaluated for survival (alive or dead) and surviving trees were measured for basal diameter (stem diameter 5 cm above the soil surface), total height (height from soil surface to the highest living apical bud). Initial measurements were taken between 1 October and 2 December for plots established in 2004, and 22 October and 2 November for plots established in 2005. Measurements after two years of growth were taken between 19 August and 26 August for plots established in 2004, and 3 September and 14 September for plots established in 2005. The predominant slope gradient of each plot was ocularly estimated with a clinometer. Where slope changed within a plot multiple slope measurements were taken and their values averaged to obtain a slope estimate.

To assist with plantation establishment, plots were sprayed with glyphosate one to three weeks prior to transplanting. Planting holes (~14 cm diameter x 21 cm depth) were opened with a post-hole digger, and 56g each of 12-24-12 fertilizer and 0-46-0 super-phosphate (NPK) was applied to the bottom of each planting hole. Two months after planting, 56g of ammonium-sulphate (20-0-0-24, NPKS) was surface applied to each tree seedling. Landowners were responsible for controlling insect pests, disease, and weeds, as they deemed necessary. There was substantial variation in landowner management. Most landowners provided a low level of management (e.g. weeding only once or twice a year, little pest control, haphazard plot inspection, occasional cattle breaches). However, a few landowners provided very high levels of management (e.g. regular clean weeding,

timely spraying for pests, regular inspection of plots). Finally, plots were fenced where protection from cattle was required.

6.3.3 On-station selection trial design

Wishnie et al. (2007) describe in detail the on-station trial's experimental design and management. In brief, three mono-specific plots of 20 trees at 3m × 3m spacing were established in each of three blocks at each location. The species studied on-station included the four species used in the on-farm trials. `Transplanting protocols (e.g. fertilization, nursery seedlings) were the same as those of the on-farm trial with transplanting occurring between 19 June and 17 July in 2003. After planting plots were manually weeded to remove competing vegetation, and pests and diseases were controlled by spraying. Weeding and spraying frequency varied with the growth rates of competitive vegetation and pest and disease incidence. The on-station trial received a consistently high-level of management (e.g. three weedings per season, timely pest control, regular plot inspection, complete exclusion of cattle). The measurement protocol was the same as that of the on-farm trial for each of the four tree species. All seedlings were initially measured between 4 July and 27 August in 2003, and measured again 2 years later between 15 June and 23 September, 2005.

6.3.4 Statistical methods

Mixed model analysis using restricted maximum likelihood and the Satterwaite degrees of freedom approximation was used to calculate probability statistics and estimate least-squared means. Tukey's test (Westafall et al., 1999) was used to assess

differences for factors involving multiple comparisons. Regardless of landowner, site was the blocking factor for the on-farm trial, while blocks were the blocking factor for the on-station trial. Block was the random effect in the mixed model. Establishment year, location, species, and their interactions were assessed for the on-farm trial as fixed effects. Species, location and their interaction effects were assessed in the on-station trial as fixed effects. Analysis was conducted separately for on-farm and on-station data sets, as well as for a combined dataset in which the effect of trial type and its interactions with other fixed factors (species and location) were specified (Table 6.1).

Plot means were used for the analysis of individual (either on-farm or on-station) datasets. However, when on-farm and on-station datasets were combined plots of the same species within the same block were averaged to give a single plot value per block for the on-station data. Establishment year was not considered when analyzing combined data. Wood volume index (1) was calculated after Newbould (1967) and scaled to wood volume per hectare assuming 1111 trees per hectare and adjusting for percent survival, using:

$$\text{Wood volume index} = \text{basal area} \times \text{height} \times 0.5 \qquad (1)$$

Wood volume was calculated for each surviving tree and then averaged to arrive at plot values. Likewise, average monthly growth rates in height and diameter were calculated by subtracting initial measurement values from the subsequent measurement value for each surviving tree, dividing by the number of days between measurements, and scaling to a 30-day month. The growth rates of individual trees were then averaged to

give plot means. Survival proportions were arc sine transformed to assist with normality. Probabilities were assessed based on the analysis of transformed proportions while mean estimates were calculated using untransformed data.

The relationship of slope gradient to survival and growth metrics was evaluated using Pearson's product moment correlation analysis (Zar, 1999). The significance of all analytical tests was assessed using an α of 0.05. The ratio of block variance to residual error variance was used to indicate the effectiveness of blocking. Large ratios indicate blocking in the experimental design is effectively accounting for variation that would otherwise have contributed to residual error variance.

6.4 Results

Across all species in both on-station and on-farm trials, final mean values after two years of growth ranged widely for survival (62-100%), basal diameter (4.8-10.8cm), height (1.8-3.2m), and wood volume index (3.6-19.7 $m^3 ha^{-1}$) (Table 6.2). Maximum least-squared mean estimates for species growth rates were produced by the on-station trial and included a 4.4mm $month^{-1}$ expansion in basal diameter for *P. quinata*, 12cm $month^{-1}$ growth in height for *S. saman*, and 0.9 m^3 $month^{-1}$ ha^{-1} increase in wood volume for *P. quinata* (Table 6.3). *Hypsipyla grandella* (Zeller) herbivory of *C. odorata* was observed at all sites in the on-farm and on-station trials.

A trial effect ($p < 0.05$), in which the on-farm trial yielded lower values than the on-station trial, was detected for all metrics with the exception of wood volume index growth rate (Table 6.1). In the on-station trial a species effect ($p < 0.01$) was detected for all metrics and a location effect ($p<0.05$) was detected for height and basal diameter

growth rates. In the on-farm trial a species ($p<0.01$) effect was detected for all metrics except wood volume index growth rate, but no location or year effects were detected. With the exception of a species by year interaction for basal diameter growth rate in the on-farm trial no interactions were detected for either the on-farm or on-station trials. The species by year interaction was due to better performance of *C. odorata* in the second year of planting (data not shown). Superior performance appeared to be related to more intensive pest management by landowners who planted *C. odorata* in 2005.

Species effects differed slightly between on-station and on-farm trials (Table 6.3). *P. quinata* and *S. saman* were found to have greater survival than *T. rosea* and *C. odorata* in the on-farm trial, whereas in the on-station trial, only *C. odorata* had low survival. *P. quinata* had the greatest basal diameter growth rate in both the on-farm and on-station trials. *C. odorata* had the lowest height growth rate in both the on-farm and on-station trials. On-station results found *P. quinata* to have the greatest wood volume index growth rate, whereas the on-farm trial results did not distinguish any species differences in wood volume index growth rate.

The location effects detected in the on-station trial indicated greater survival as well as basal diameter and height growth rates at the Los Santos (high rainfall) location. Confidence intervals were wide for all metrics with the exception of height growth rate for both the on-farm and on-station trials. Confidence intervals for wood volume index growth rates were particularly pronounced and extended into negative values for a number of species.

Blocking in the on-station trial resulted in ratios of block to residual error variance averaging 0.72 with a range of 0.41-1.0. In contrast, blocking in the on-farm

trial generally produced higher ratios with an average ratio of 1.06 and a range of 0.34-2.48. Slope gradients of individual plots in the on-farm trial ranged from 0-75%. When assessed across all species and sites, plot slope gradient was negatively correlated with survivorship ($r=-0.37$, $p<0.01$), basal diameter growth rate ($r=-0.41$, $p<0.01$), height growth rate ($r=-0.46$, $p<0.01$), and wood volume index growth rate ($r=-0.34$, $p<0.01$).

Implementation of the multi-location on-farm trial resulted in a number of practical lessons. Landowner preferences as well as space and management restrictions required the on-farm trial design be flexible with regards to experimental balance, randomization procedures, plot size, plot shape, and management practices. High fixed establishment costs (labour, infrastructure, and capital) when working with multiple landowners required recruiting landowners over a number of years. Despite fencing, livestock breaches occurred at 23% of sites. Coordination of measurement activities with landowners, project labour supply, and equipment availability resulted in unequal measurement intervals. Measurement conditions were often poor (steep slopes, weedy conditions) and made locating trees difficult.

6.5 Discussion

Maximum values for growth metrics indicate substantial growth is obtainable in just a few years for the four tree species examined. A number of studies have evaluated early growth in *C. odorata* (Gerhardt, 1998; Griscom et al., 2005; Navarro et al., 2004; Piotto et al., 2004), *P. quinata* (Mengel et al., 1993; Pérez-Cordero et al., 2003), *S. saman* (Jama et al., 1989; Piotto et al., 2004; Tolkamp and Adrianto, 1998), and *T. rosea* (Butterfield and Espinoza C, 1995). The results of the present study fall within the range

of values reported in these studies. To date, no multi-location trial has compared these species and information on the plantation performance of these species in Panama is lacking.

Both the on-farm and on-station results indicate *C. odorata* had poorer initial survival, and in many cases growth, compared to the other species. The poor performance of *C. odorata* may be related to its susceptibility to *Hypsipyla grandella* Zeller, which unless rigorously controlled results in death (lower survival) and die-back (lower height growth). *H. grandella* herbivory of *C. odorata* is a well-recognized problem in plantation forestry (Cornelius and Watt, 2003) and requires very intensive management to control properly. As such, *C. odorata* may not be an appropriate plantation species for landowners unless very high levels of management can be provided.

Detection of superior tree performance on-station in this study is consistent with similar findings for on-farm horticultural crop trials (Riley, 2000). The on-farm and on-station trial were generally similar in their detection of species effects for survival and growth. The only differences were comparatively lower survival for *T. rosea* and the lack of a species effect for wood volume index growth rate in the on-farm trial. The species by year interaction detected in the on-farm trial, appeared to result from better management of *C. odorata* by landowners establishing plots in 2005. This reflects the importance of working with a sufficiently large landowner cohort when conducting on-farm trials.

Better performance on-station is likely due to differences in management between on-station and on-farm trials. Although some landowners provided exceptionally high

levels of management to their plots, on average, on-farm sites received a lower level of management than the on-station trial. The poorer survival of *T. rosea* on-farm may be related to pest pressure, as evidenced by desiccated leaves and swollen branches, which is likely to be more effectively controlled by the on-station management regime.

On-farm and on-station trial results did differ markedly in the detection of a location effect. Detection of a location effect in the on-station trial only may be the result of poor site conditions at 1 of the 2 locations in this trial. Specifically, the on-station trial at Río Hato was located on a particularly poor site that had soil compaction. In contrast, the on-farm sites at Río Hato captured a wider range of soil conditions ranging from poor to adequate. One of the strengths of on-farm trials is that they permit sampling of a broader range of environments that may not be available at select research stations (Gomez and Gomez, 1984).

The higher ratio of block to residual error variance in the on-farm trial compared to the on-station trial suggests blocking was more effective in the on-farm trial. The process of blocking in the on-farm trial captured differences in site and management characteristics. In contrast, blocking in the on-station trial only captured variation between blocks at a single site under a single management regime. Furthermore, the large blocks in the on-station trial may have been less effective because within block variation in large blocks can be as substantial as between block variation (Dempster et al., 1977). Use of incomplete block designs in forestry can help ameliorate the issue of large blocks (Dempster et al., 1977). Alternatively, assessment of micro-variability (e.g. soil variability) within blocks can yield spatial covariates that improve parameter estimation

(Fagroud and Van Meirvenne, 2002). In contrast, on-farm trials usually benefit most from increasing the number of farm replicates (Fielding and Riley, 1998).

Lower growth estimates, lack of a location effect, greater blocking efficiency, broader inference space, and confidence intervals paralleling those of the on-station trial, all suggest estimates for survival and initial growth rates obtained from the on-farm trial are more realistic than those of the on-station trial. Thus, while on-station trials may indicate the potential of timber species under select, optimum conditions, on-farm results may be more useful for assessing the potential of native timber species plantations for landowners' conditions.

Wood volume index data were highly variable. This appears to be at least in part, because wood volume index is a synthetic variable integrating survival, height growth, and basal diameter growth, which are all positively correlated metrics during initial growth (data not shown). As such, wood volume index tends towards more extreme values than each metric on its own. Negative growth rates in wood volume index at the plot level, although rare, were largely the result of mortality reducing wood volume at the plot level despite continued growth. However, negative growth in height was also observed at the plot level in the case of *C. odorata* and appeared to be related to herbivory by *H. grandella*. Machete damage during weeding also resulted in negative growth in height being recorded for individual trees, irrespective of species, but damage was never widespread enough to result in negative growth at the plot level.

Slope gradient has been found to be negatively correlated with soil chemical fertility (de Castilho et al., 2006) and is potentially an easily collected surrogate for site quality (Vanclay, 1992). However, slope gradient may underestimate the contribution of

specific soil properties to observed variation (Hall et al., 2004). The negative correlation between slope gradient and growth detected in this study is in agreement with the observation that steep slopes negatively affect tree growth in the tropics (Lieberman and Lieberman, 1987). However, the consistently low correlation coefficients belie the indirect and imprecise relationship between slope gradient and site quality.

Practical lessons learned about conducting a long-term on-farm agroforestry trial parallel those of on-farm trials for annual crops. Lack of experimental balance (Spilke et al., 2005), problems of randomization (Fielding and Riley, 1998), irregular plot size and shape, as well as variable management practices (Gomez and Gomez, 1984), are well-recognized issues in the on-farm trial literature for annual crops. On-farm trials are labor intensive and two full-time scientists are usually required to manage 15-25 sites in a year (CIMMYT, 1982). This study partially resolved this problem by spreading establishment of the on-farm trial over two years. Livestock damage in on-farm agroforestry trials has been reported (Borel and Romero, 1991), but estimates of frequency of occurrence have not been provided. Our study suggests livestock breaches of fencing are common in grazed landscapes, and while likely to decrease tree performance, are also representative of a realistic hazard during plantation establishment.

Rapid initial growth, uneven growth intervals, and an unbalanced design required standardization of growth to a monthly rate to prevent confounding treatment effects with differential growth periods. Measuring trees during the dry season when growth is partially arrested can help remedy this practical concern because differences in growth periods do not result in substantial differences in final measurement values.

Permanently marking trees to facilitate periodic measurement is a consideration in on-farm agroforestry trials (Rao and Coe, 1991). Our study preferred aluminium to plastic tags because the uncontrolled spread of fire due to pasture burning is a common risk in tropical agricultural landscapes (Fearnside, 2000). However, plastic ribbon is better than metal wire for attaching tags because it stretches with tree growth. Plastic ribbon must be periodically replaced because it melts due to fire, can be cut during weeding, and becomes brittle with exposure. Maps were especially helpful because tree identity and location were often obscured due to mortality, lost tags, and heavy weed conditions. Although some lessons are specific to agroforestry trials, in general on-farm trials for annual crops appear to be a rich source of practical information for the design and management of on-farm agroforestry trials.

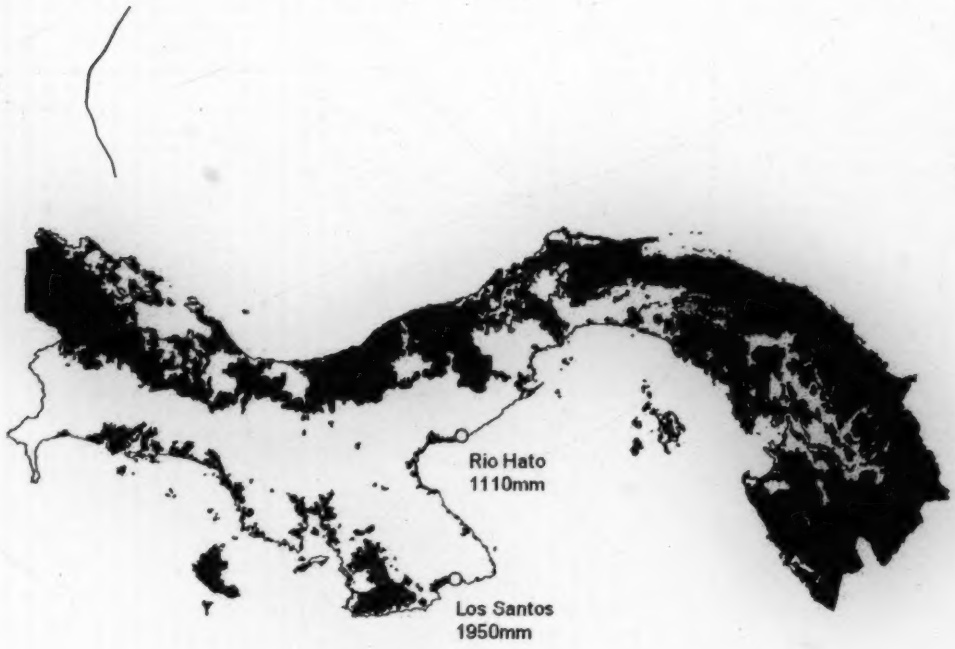
6.6 Conclusions

Initial growth for native timber species under plantation conditions in Panama can be substantial, but also highly variable. On-farm results are more conservative (lower growth estimates, no location effect) than on-station results. Lower estimates are likely the result of on-farm management being less intensive than on-station management. Lack of a location effect may be due to better representation of possible site conditions in the on-farm trial, or alternatively the result of more variable management masking a location effect. As such, on-farm trial estimates, rather than on-station results, are more likely to approximate the performance of native timber plantations when established by farmers. Blocking was more efficient in the on-farm trial than the on-station trial and plot slope gradient in the on-farm trial was found to affect tree growth in the expected

negative manner. Across the on-station and on-farm trial *C. odorata* tended to have poor initial survival and growth that appeared to be related to herbivory by *H. grandella*. This calls into question the appropriateness of *C. odorata* as a plantation species for landowners who may not be able or willing to provide high-levels of plantation management. Lessons learned during the management and design of the on-farm trial paralleled those for on-farm trials of annual crops. Although, on-farm testing is only an intermediate step between researcher management and actual farmer management these results highlight the importance of on-farm testing for developing timber species recommendations for landowners in Panama.

6.7 Figures

Figure 6.1 Map showing forest cover (shaded areas) in Panama in 1992, and the location and rainfall (mm year^{-1}) of the two experimental areas: Los Santos and Rio Hato for on-station and surrounding on-farm trials (ANAM, 1992 map produced from SIG Republic, Eon Systems, all rights reserved).



6.8 Tables

Table 6.1 P-values for fixed factors in mixed model analysis of on-farm, on-station, and combined datasets of four native-timber species grown in Panama at two locations.

On-farm analysis fixed effects	Survival	Height growth rate	Basal diameter growth rate	Wood volume index growth rate
Year	0.76	0.74	0.73	0.99
Location	0.46	0.29	0.51	0.51
Species	< 0.01**	< 0.01**	< 0.01**	0.07
Species x Location	0.64	0.13	0.62	0.98
Species x Year	0.15	0.07	< 0.05*	0.53
Location x Year	0.75	0.83	0.73	0.44
Species x Location x Year	0.61	0.15	0.16	0.36
On-station analysis fixed effects				
Species	< 0.01**	< 0.01**	< 0.01**	< 0.01**
Location	0.65	<0.05*	< 0.05*	0.05
Species x Location	0.08	0.42	0.15	0.05
Combined analysis fixed effects*				
Trial type	<0.05*	< 0.05*	< 0.01**	0.17
Species				
Location				
Trial type x Species				
Trial type x Location				
Species x Location				
Trial type x Species x Location				

* = $p<0.05$

** = $p<0.01$

Note: The hypothesis being tested for the combined analysis is the presence of a trial type effect only. Thus, p-values are only given for the trial type fixed factor. All other fixed factors are included to illustrate the structure of the mixed model only.

Table 6.2 Average final basal diameter, height and wood volume index after two years of growth on-station and on-farm in Panama, for each of four native timber species planted at Rio Hato and Los Santos.

Species	Trial type	Survivorship (%)	Basal diameter (cm)	Height (m)	Wood volume index (m3 ha-1)
C. odorata	On-farm	62	5.8	1.8	3.6
	On-station	64	7.3	2	4.5
P. quinata	On-farm	86	7.3	2.4	11.5
	On-station	100	10.8	2.9	19.7
S. saman	On-farm	87	4.8	2.7	4
	On-station	99	6.4	3.2	6.8
T. rosea	On-farm	69	5.2	2.3	4.3
	On-station	87	6.9	3	7,1
Location					
Los Santos	On-farm	80	6.4	2.7	6
	On-station	89	9.5	3.4	14.9
Rio Hato	On-farm	72	5.2	2	6
	On-station	86	6.1	2.1	4

Table 6.3 Least-squares means and 95% confidence intervals (CI) for average monthly growth increment in basal diameter, height, and wood volume index during the first two years of growth for each of four native timber species planted on-farm and on-station at two locations in Panama. Results are for mixed model analysis conducted separately for on-farm and on-station trial data, as well as for combined data. Treatments followed by different letters differ significantly ($P \leq 0.05$); within a column lowercase letters compare species while uppercase letters compare locations or trial types.

		Survival (%)		Basal diameter growth rate (mm month^{-1})		Height growth rate (cm month^{-1})		Wood volume index growth rate (m^3 month^{-1} ha^{-1})	
Trial type	Species/Location/Trial type	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
On-farm	*C. odorata*	64 b	54-73	1.7 b	1.2-2.2	5.6 b	3.8-7.3	0.17 a	-0.1-0.43
	P. quinata	85 a	76-93	2.4 a	1.9-2.8	6.8 a	5.1-8.4	0.49 a	0.26-0.71
	S. saman	87 a	76-98	1.6 b	1.1-2.2	9.0 a	7.1-10.8	0.13 a	-0.16-0.43
	T. rosea	71 b	60-82	1.4 b	0.8-2.0	7.0 a	5.1-8.8	0.15 a	-0.15-0.45
	Los Santos location	80 A	71-90	1.9 A	1.4-2.4	7.5 A	5.6-9.5	0.25 A	0.03-0.48
	Rio Hato location	73 A	63-83	1.7 A	1.1-2.3	6.6 A	4.4-8.9	0.21 A	-0.03-0.46
On-station	*C. odorata*	64 b	50-79	2.8 b	0.9-2.5	7.8 b	5.9-9.6	0.20 b	-0.18-0.53
	P. quinata	100 a	86-100	4.4 a	3.5-5.1	11.0 a	9.2-12.8	0.90 a	0.61-1.18
	S. saman	99 a	85-100	2.5 b	1.7-3.3	12.3 a	10.5-14.1	0.30 b	0.01-0.59
	T. rosea	87 a	73-100	2.7 b	1.6-3.2	11.8 a	10.0-13.6	0.31 b	0.02-0.6
	Los Santos location	89 A	74-100	3.9 A	2.4-4.5	13.5 A	11.0-16.0	0.68 A	0.32-0.1.03
	Rio Hato location	86 A	71-100	2.3 B	0.9-3.0	7.9 B	5.4-10.4	0.18 A	-0.18-0.53
Combined	*On-station trial*	88 A	77-100	3.1 A	2.4-3.8	10.7 A	7.9-13.5	0.43 A	0.17-0.68
	On-farm trial	76 B	69-82	1.8 B	1.4-2.1	7.1 B	5.7-8.5	0.23 A	0.09-0.37

7.0 Tree seedling establishment in living fences: a low-cost agroforestry management practice for the tropics[14]

7.1 Abstract

Establishing trees in pastures can have production and conservation benefits, but is complicated by the presence of livestock. The need to protect seedlings from livestock increases establishment costs, which in turn, can deter landowners from planting trees. Living fences are an ubiquitous feature of pasture landscapes in the tropics. This study quantified the effectiveness of a living fence to protect tree seedlings during the first 2 years after planting. Planting seedlings of four native tree species [*Cedrela odorata* L., *Pachira quinata* (Jacq.) W.S. Alverson, *Samanea saman* (Jacq.) Merr., and *Tabebuia rosea* (Bertol.) A. DC.] into a living fence provided protection from livestock except in cases where tree species were palatable to livestock (i.e. *P. quinata*). Most species planted into the living fence had greater survival (62% versus 28%), relative growth (10.3 versus 5.8), and final height (191cm versus 108cm) compared to those planted in open-pasture. However, the survival and growth of tree seedlings planted into the living fence was lower than at a nearby plantation with no livestock, regular weeding, and no living fences. The use of living fences as a protective barrier appears to be an effective low-cost approach for establishing trees in tropical pasture landscapes.

[14] This chapter as developed by B. Love, E.W. Bork, and D. Spaner has been submitted to *Agroforestry Systems*.

7.2 Introduction

7.2.1 Tree establishment in pastures

Introducing trees into pastures is an important production and conservation objective (Bellefontaine et al., 2002; Long and Nair, 1999). Potential benefits include: diversified production and income; increased total productivity; maintenance of tree biodiversity; the provision of shade and browse for livestock; and the provision of refugia for natural biodiversity. In Panama, pasture landscapes are especially important because they have replaced 70% of the native forest (Ledec, 1992).

Establishment of trees in pastures can be difficult. Tree seedlings in grazed pastures can be damaged by cattle browsing and trampling (Pitt et al., 1998). Physical barriers (Beetson et al., 1991) or abrasive substances and chemicals (Eason et al., 1996) can be used to protect trees from livestock damage. All these protection strategies increase the costs of tree establishment, and physical barriers can result in poor seedling development (Beetson et al., 1991). In developing countries, landowners prefer low-cost establishment methods for planting trees (Arnold and Dewees, 1998) and increased establishment costs may deter tree planting.

7.2.2 Living fences

Living fences consist of closely-spaced contiguous trees that delimit a field boundary to which fencing material (usually barbed wire) may be attached (Budowski, 1993; Budowski and Russo, 1993). Living fence stakes are vegetatively propagated to form fences (Zahawi, 2005), although pre-existing trees may be incorporated into the fence line. Increases in fencing, driven by improved availability of modern fencing

materials (e.g. high tensile wire), have made living fences a widespread feature of tropical agricultural landscapes in Latin America (Budowski, 1987). Living fences in Central America have been found to account for as much as 45% of all fencing, and cover up to 50.5 linear meters per hectare (León and Harvey, 2006). Additionally, landowners are accepting of establishing trees in living fences (Borel and Romero, 1991). Planting trees along field edges is more acceptable to landowners than planting in the interior of existing fields because potential interference with field crops is reduced.

Electrified fencing protects tree seedlings planted directly underneath it from livestock (Lehmkuhler et al., 2004). Living fences could provide similar low-cost protection to tree seedlings during establishment by acting as a robust physical barrier to livestock. However, because animals seek boundaries upon entering fields and rest in shade during the day (Stuth, 1991), saplings near the field edge may continue to be at risk of damage at certain times. Additionally, tree species' palatability is variable (Kaitho et al., 1996) and certain species may be more prone to browsing. Living fences may also compete with seedlings for above- and below-ground resources, as demonstrated by competition studies in alley-cropping systems (Jose et al., 2004). While natural recruitment of trees into living fences is common, little field research has investigated deliberate strategies to employ living fences as a protective environment into which tree seedlings may be planted.

7.3 Materials and methods

7.3.1 Study site

A field experiment was established in El Cacao township of Tonosí Province in the Republic of Panama (Figure 7.1). The study area was located 50 m.a.s.l, in Holdridge's (1967) humid tropical forest life zone, and has an average annual precipitation and temperature of 2000 mm and 27°C, respectively (IGNTG, 1988). There is a pronounced five-month dry season that begins in January. The pasture where the experiment was situated is ~ 4.5 ha in size, topographically flat, and bound on all four sides by a living fence with a total length of 900 m. The pasture consisted of a pure sward of African star grass (*Cynodon nlemfuensis* Vanderyst), a creeping stoloniferous pasture grass. The soil was arable, dark brown in color, of clay texture, and became massive and cracked upon drying.

The pasture was grazed once a month during the rainy season (June-December) by 20-30 cattle for periods ranging from 3-10 days, and about every two months during the dry season by 15-20 cattle for periods ranging from 3-7 days. The pasturing cattle were Zebu (*Bos indicus*) and *Bos indicus* x *Bos taurus* crosses. Stocking density averaged 5 cattle per hectare during the rainy season and 3.3 cattle per hectare during the dry season. Overall, grazing intensities were considered light during the dry season and light to moderate during the rainy season. At no time did the pasture sward show signs of overgrazing (e.g. bare ground, erosion, pugging). At the beginning of each rainy season (June – July) the pasture is sprayed with a single application of 2,4-D to control broadleaf weeds using a backpack sprayer. A 1m buffer zone adjacent to all planted tree seedlings

was left unsprayed. The living fence used in this investigation consisted largely of living stakes with boles of ~ 2 m high that were pollarded once annually during the dry season.

7.3.2 Experimental design

Single-tree seedling plots (Huxley, 1987) were arranged in a completely randomized design. The study was a factorial experiment with four native tree species planted at two positions within the pasture (i.e. in a living fence or within open-pasture). Fifteen replicate plots were established for each species at each planting position (n=120). The tree species evaluated were: Cedro Amargo - *Cedrela odorata* L., Cedro Espino - *Pachira quinata* (Jacq.) W.S. Alverson, Guachapalí - *Samanea saman* (Jacq.) Merr., and Roble - *Tabebuia rosea* (Bertol.) A. DC.

7.3.3 Field methods: living fence planting

Tree seedlings were planted on 10 August 2004 during the early part of the wet season. Seedlings were produced in a nursery three months prior to planting using soil plugs (low-nutrient mix: sand, rice hulls, and black soil) in trays. Average seedling heights (± 95% confidence interval) at planting were 26 ± 2.6 cm, 19 ± 1.8 cm, 20 ± 2.2 cm, and 18 ± 0.7 cm for *C. odorata, P. quinata, S. saman,* and *T. rosea*, respectively. Seedlings were planted at regular intervals (3m) in a linear fashion into both a living fence (directly below barbed wire) and open-pasture at a 10 m distance from the living fence (Figure 7.2). No physical or chemical protection was provided to seedlings planted in open-pasture. All seedlings were numbered in their trays and the PLAN procedure in SAS (SAS, 2005) was used to randomly assign each seedling to a planting site.

Planting holes (~14 cm diameter x 21 cm depth) were opened with a post-hole digger and 32 g each of 12-24-12 fertilizer and 0-46-0 super-phosphate was applied to the bottom of the holes and covered with earth before planting. When planting sites at 3m intervals conflicted with a living fence post they were shifted along the fence up to 15 cm, to avoid planting directly on top of living stakes. A square-area of $1m^2$ was manually weeded to clear *C. nlemfuensis* (African star grass) from around each seedling prior to planting. At planting, carbofuran (2,3-dihydro-2,2-dimethyl-7-benzofuranyl methylcarbamate) was surface applied 2 cm from the stem to all seedlings to control white grub (*Phyllophaga* Harris), a common insect pest of the area. Fertilizer application and white grub control were used to mimic standard forest plantation establishment protocols for the region. White grub was only observed at four planting sites in the living fence and three planting sites in open-pasture.

Areas around tree seedlings were subsequently manually clean-weeded ($1m^2$ around seedlings) of all vegetation, including *C. nlemfuensis*, on 11 January 2005 and 16 June 2005. Tree seedlings were measured six times: 11 August, 2 September, and 30 December of 2004; 16 June of 2005; and 14 January and 21 July of 2006. The total time period during which measurements were taken lasted 709 days (~ 2 years). Survival, symptoms of livestock damage (i.e. trampling, defoliation, and rubbing), and seedling height (height from soil surface to the highest living apical bud) were recorded during all measurement periods. Basal diameter (stem diameter 5cm above the soil surface) was recorded from 16 June 2005 onwards.

Hoof impressions in the soil combined with bark scarring on the lower bole were used to identify trampling. Torn leaves and sheared stems were used as indications of

browsing and were easily distinguished from insect herbivory. Abrasion and hair deposits on the upper bole were used as evidence of animal rubbing. At the end of the experiment, two experts, both of whom have worked with over 90 plantation plots of the tree species being tested in this trial, evaluated seedlings for acceptable timber production characteristics (e.g. height, bole development). Each tree's conformation was rated as either acceptable or unacceptable.

The closest living fence stake on each side of every planted seedling was characterized at the end of the experiment. Measurements for living stakes included: distance to seedling, species, basal area, and height. Height was measured to the tip of the tallest branch prior to pollarding after one-year of growth. Basal area was calculated from basal diameter assuming a circular bole.

7.3.4 Field methods: plantation planting

The same four tree species described above were planted in mono-specific plantation plots at a nearby site (~ 0.5 km away) at the same time in 2004. The plantation was part of the Native Species Reforestation Project's on-farm trial involving 24 landowners at two locations within Panama (PRORENA, 2006). These plots received plantation type management (manual clean weeding three times a year) and the site was free of competition from living fences as well as protected from livestock with fencing. The plantation site was on a slope that varied from 7 - 21% and was bordered by secondary forest growth. Soils were lighter in color, contained less clay, and did not crack upon drying in comparison to the living fence trial site. Tree planting used the

same procedures described above, except trees were planted in a 3m x 3m regular grid pattern. Sixty trees from each mono-specific plot were measured after 2 years of growth.

7.3.5 Statistical analysis

Descriptive statistics (simple means and 95% confidence intervals) were calculated to describe living fence characteristics and tree growth under plantation conditions. Mixed model analyses based on maximum likelihood estimation were used to model variance heterogeneity while: 1) computing least squared means and 95% confidence intervals for relative growth and final measurements of height and basal diameter based on surviving trees, and 2) assessing the significance of differences in relative growth and final size measurements using Tukey's test (Day and Quinn, 1989) for multiple comparisons based on surviving trees, where applicable. Both species and planting position were analyzed as fixed effects and Akaike's information criterion (Akaike, 1974) was employed to evaluate whether variance modeling was warranted. Relative growth was calculated as the final size measurement divided by the initial size measurement at time of planting (e.g. Relative growth in height = Final height / Initial height).

Contingency tables and a Fisher's two-way exact test were employed to assess the statistical significance of observed differences in count data (survival, acceptable tree seedlings for timber production, cattle damage) using the FREQ procedure in SAS (Stokes et al., 1995). Significance of the overall responses to planting position when considering all tree species was evaluated using the Mantel-Haenszel statistic (Mantel and Haenszel, 1959) where data satisfied the Mantel-Fleiss criterion (Mantel and Fleiss,

1980). Odds-ratios for overall association were calculated for data satisfying the Breslow-Day test for homogeneity (Breslow and Day, 1980). A two-tailed t-test was used to evaluate the significance of differences in growth between seedlings damaged by cattle and those that were not. Statistical Analysis System (SAS, 2005) software was used to conduct all statistical analyses, using either mixed models (Littell et al. 1996) or categorical data analysis (Stokes et al. 1995).

7.4 Results

7.4.1 Living fence characteristics

Of the 120 living stakes neighboring seedlings planted within living fences, there were 62 *Spondias mombin* L., 51 *Jatropha curcas* L., three *Gmelina arborea* Roxb. ex Sm., two *Guazuma ulmifolia* Lam., and one each of *T. rosea* and *Cordia alliodora* (Ruiz & Pv.) Oken. All these species are semi-deciduous to deciduous in habit. On average, living stakes were 106 cm distant from planted seedlings and had an average basal area and height of 48 cm^2 and 3.1 m, respectively (Table 7.1). Characteristics of the living fence examined in this study are typical of the stake size and density found in other living fences observed in the region (pers. obs.).

7.4.2 Seedling survival and acceptability

Three and a half months after planting there was a sharp decline in tree seedling survival, with survival being lowest in open-pasture (Figure 7.3). After 2 years, 62% of planted seedlings in the fence had survived compared to only 28% of those planted in

open-pasture. Survival continued to decline slightly toward the end of the 2 years of observation in both the living fence and the open-pasture treatments.

Survival also differed between planting locations on the basis of the identity of the planted tree species (Figure 7.4). Seedling survival was greater ($p < 0.05$) in fences, but only for *P. quinata*, *C. odorata*, and *T. rosea*. Overall survivorship at the end of the trial was markedly greater within the living fence ($p<0.0001$), with the odds of tree seedlings surviving being 9 times higher in the living fence than in open-pasture. However, survival in the living fence remained 16% lower than the survival observed at the nearby monoculture plantation (Table 7.2), and was particularly low for *P. quinata* (33% in the living fence vs. 75% in the plantation).

Survival alone provides no indication of whether the performance of tree seedlings is "acceptable" for timber production (as defined in methods). *C. odorata* and *P. quinata* produced no acceptable seedlings in either open-pasture or the living fence, while *T. rosea* and *S. saman* had significantly more acceptable seedlings ($p < 0.01$) when planted within the fence (Figure 7.5).

7.4.3 Absolute and relative growth performance

Relative growth in seeding height differed by tree species ($p = 0.0009$) and planting location ($p = 0.02$) (Figure 7.6). Similarly, final tree heights differed by tree species ($p = 0.0003$) and planting location ($p = 0.01$) (Table 7.2). While seedlings of all species except *C. odorata* were taller within the living fence than in open-pasture at the end of the trial (Table 7.2), most tree species (all but *S. saman*) planted in the living fence remained shorter than those observed in the nearby plantation (Table 7.2). All species

except *C. odorata* exhibited greater relative growth in height during the study period when planted within the living fence (Figure 7.6).

Mean final measurements and relative growth in basal diameter differed by species but not by planting position (Table 7.2). Similar to the height responses, the final basal diameters of trees planted within the living fence were lower compared to those observed in the nearby plantation with the exception of *S. saman* (Table 7.2).

7.4.4 Cattle damage

Livestock damage to seedlings during the experiment included trampling, browsing, and rubbing. Over the course of six observation periods, a total of 44 trampling, 28 browsing, and 3 rubbing events, as indicated by symptoms, were observed across all planted tree seedlings. Most of the trampling damage (77%) occurred in the first month, while browsing occurred throughout the study, and rubbing was only observed during the last measurement when trees were taller (data not shown). *P. quinata* was the most frequently browsed species accounting for 89% of all browsing events. More cattle damage occurred within the open-pasture (71%) compared to within the living fence (29%) ($p < 0.0001$). The odds of trees planted in the open-pasture being damaged by cattle was more than 5 times greater than for trees planted within the living fence. While trampling was highly associated with planting in open-pasture for all species ($p < 0.0001$), no association was detected between browsing and planting location for *P. quinata* ($p = 0.71$). Finally, seedlings planted within the living fence that were damaged by cattle during the study produced less relative growth ($p < 0.05$). On average

undamaged trees were 12 times taller than their initial height, while damaged trees were only 6 times taller on average.

7.5 Discussion and conclusions

Greater survival, greater relative growth in height, lower cattle damage, and the negative effect of cattle damage on relative growth in height within the living fence, collectively suggest the fence acted as a protective environment for planted seedlings. The short height of trees in open-pasture after two years makes continued mortality probable because seedlings are unable to escape trampling and browsing in that condition. Additionally, continued browsing of *P. quinata* in the living fence makes further mortality of this species probable at this location. Mortality was most pronounced at the beginning of the study, a pattern that is commonly observed in experiments examining tree seedlings damaged by livestock (Lewis, 1980).

While growth in height was significantly lower in open-pasture than in the living fence, no difference was detected in basal diameter. Coupled with a much greater incidence of livestock damage in open-pasture, this suggests the primary impact of livestock damage is to inhibit height growth rather than basal diameter growth. It was observed that trampling broke stems and damaged apical meristems. This reduced seedling height and resulted in bushy growth habits with robust leafy crowns. Although this habit is not acceptable for timber production it appears to maintain early growth in basal diameter despite trampling stress.

Based on observations from the adjacent plantation it appears likely that seedlings established in living fences will have lower growth and higher mortality compared to

plantation seedlings grown with no neighboring vegetation and free of cattle grazing. Thus, while the living fence acts as a nurse crop in grazed pasture, it may also impose competition and reduce the growth of seedlings compared to ungrazed conditions free of living fences. Quantification of this potential competitive effect requires an experimental design where plantation management is not confounded with location, as is the case in the present study. Only *S. saman* and *T. rosea* produced trees of acceptable conformation for timber production when planted in the living fence. *S. saman* was the only species to exhibit height and basal diameter growth comparable to that observed in the nearby plantation.

Nevertheless, after only two years of growth in the living fence, both *S. saman* and *T. rosea* had average heights of 3 m and 2 m, and were 16 and 11 times taller than their initial heights, respectively. This indicates substantial growth can be achieved in a living fence even if it is lower than growth observed under plantation conditions. Moreover, the low management and opportunity costs of establishing trees in a living fence may compensate for reduced survival and growth. Total costs for planting 60 seedlings in a living fence amounted to ~ US $25 or 42 cents a tree ($15 for seedlings, fertilizer, and pesticides; plus two workdays at US $5/day), with no further expenditures expected for stand maintenance. Capital outlays could be further reduced if farmers produced the seedlings themselves and provided their own labor. In contrast, plantation establishment costs in Panama are ~ US $2000 ha^{-1} (US $1.90/tree) (Zanin, 2005). Perhaps most important, the strategy of tree production employed by this study required no modification in pasture management. For trees planted in open pasture, growth could be improved by removing livestock initially, and then reintroduced after trees are robust

enough to resist cattle damage. However, the opportunity cost of losing access to grazing land prohibits use of this strategy. Cash poor farmers need low cost strategies that do not require modification of pasture management in order to produce timber.

Trampling damage was most pronounced early in the experiment in open-pasture when seedlings were numerous and small. Living fences provided protection from trampling because cattle could not trample seedlings unless physically contacting the overlying fence. In contrast, browsing occurred throughout the experiment both in open-pasture and the living fence because tree heights under 2 m and living fence barriers did not prevent browsing. The poor performance of *P. quinata* in the living fence appears to be related to sustained browsing by cattle. Concentration of browsing on *P. quinata* was likely due to its salty tasting foliage, which local ranchers recognize as being palatable to cattle. Surveys of grazed areas provide floristic evidence that *P. quinata* is browsed by cattle (Stern et al., 2002). This finding suggests highly palatable tree species will not be able to achieve acceptable growth even if planted in living fences, unless livestock grazing is reduced or ceases. Rubbing only occurred towards the end of the experiment because trees must be tall enough (> 2m) for rubbing to occur.

In addition to seedling palatability, many other factors affect livestock behavior and may therefore affect incidences of browsing and trampling. For example, foraging patterns and preferences change with type of animal (Kronberg and Walker, 1993), grazing pressure (Parsons et al., 1991), pasture composition (Heady and Torell, 1959), as well as general climate and field topography (Heady, 1964). Cattle seek and follow linear boundaries (Stuth, 1991) and lines of planted trees may be more easily encountered and followed by livestock than random patterns. Lignification increases with seedling

age (Hellmuth, 1969), is correlated with reduced palatability (Heady, 1964), and may increase resistance to trampling or defoliation when it results in increased tensile strength (Dockrill et al., 2006; Read and Stokes, 2006). Living fences vary in species composition (Budowski, 1987) and physical attributes such as density (León and Harvey, 2006), which may affect the level of competition with planted seedlings.

The microsite environment experienced by seedlings in a living fence can be highly variable. Even in this study there was substantial variation in distance to the nearest living stake as well as the basal area, height, and species identity of living stakes. Assessment of how microenvironment characteristics affect growth could assist in the refinement of decision-making rules to guide landowners in successfully establishing seedlings within living fences. Traditionally, foresters have used basal area as a surrogate for competition (Bella, 1971), in part because it is easily measured and is known to correlate with tree crown growth and sapwood area. However, the regular pollarding of living fence stakes to 2 m height makes the measurement of new growth possible. New crown growth may be more highly correlated with leaf area (i.e. light competition) and root biomass (i.e. below ground competition for nutrients and water) than basal area, and as a result, could be considered as a surrogate for assessing competition effects in living fences.

Our study suggests the need for further research into a larger suite of tree species planted into living fences and pastures of varying characteristics in different agro-ecological zones. On-farm trials (Stroup et al., 1993) permit collaboration with local landowners and may assist researchers in gaining access to a diverse range of living fences (species, density, age) and site conditions (soils, slope, grazing practices) that may

not be available at existing research stations. Additionally, using landowner evaluations (Franzel et al., 1996) can help identify tree species with acceptable growth and management requirements. Palatability screening with penned livestock (Kalio et al., 2006) prior to species selection for field trials could focus testing on species of low palatability and thereby increase the probability of identifying species that perform well in living fences.

The results of this study lead us to conclude: 1) Living fences can protect seedlings from damage by livestock, and while this increases the survival and growth of planted trees it does not necessarily result in growth that is acceptable for timber production. 2) Tree species that livestock prefer to browse (i.e. *P. quinata*) are not appropriate for planting into pastures, including bordering living fences. 3) Tree survival and height growth for trees planted in the living fence were lower than growth and survival observed at a nearby plantation with the exception of *S. saman*, but low management costs and minimal land use competition relative to plantations may make living fence plantings acceptable to landowners seeking low-cost timber production strategies (e.g. cash poor farmers). 4) Of the four species evaluated, *S. saman* appears to be the most appropriate candidate for planting into living fences.

7.6 Figures

Figure 7.1 Geographical location of the El Cacao experimental site in the Republic of Panama.

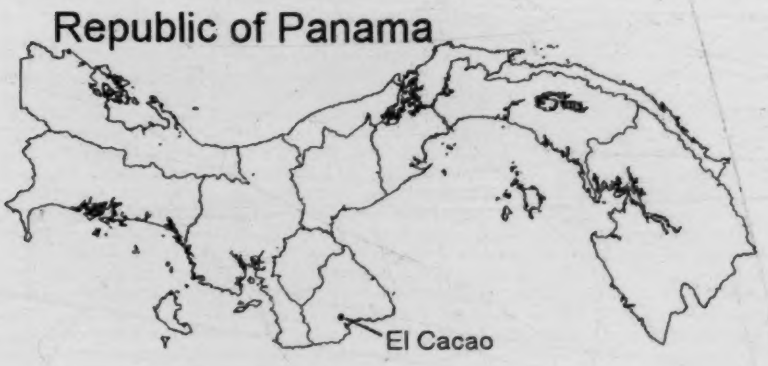
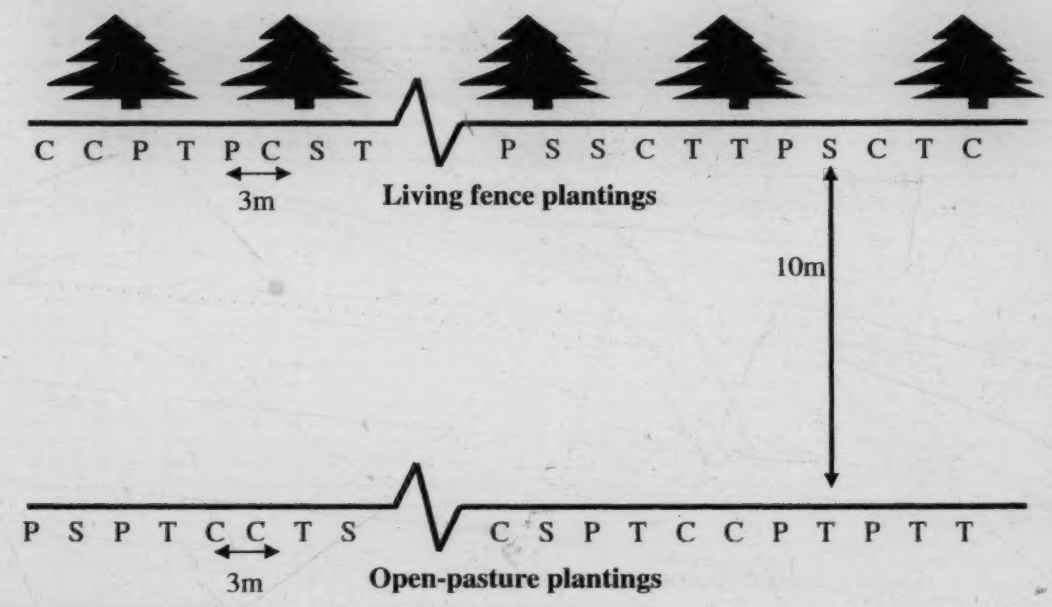


Figure 7.2 Layout of experimental plots in the living fence field trials in Panama, 2004-2006.



Legend
C = *C. odorata*
P = *P. quinata*
S = *S. saman*
T = *T. rosea*

Figure 7.3 Total survival of tree seedlings planted in either living fences or open pasture in Panama, 2004-2006.

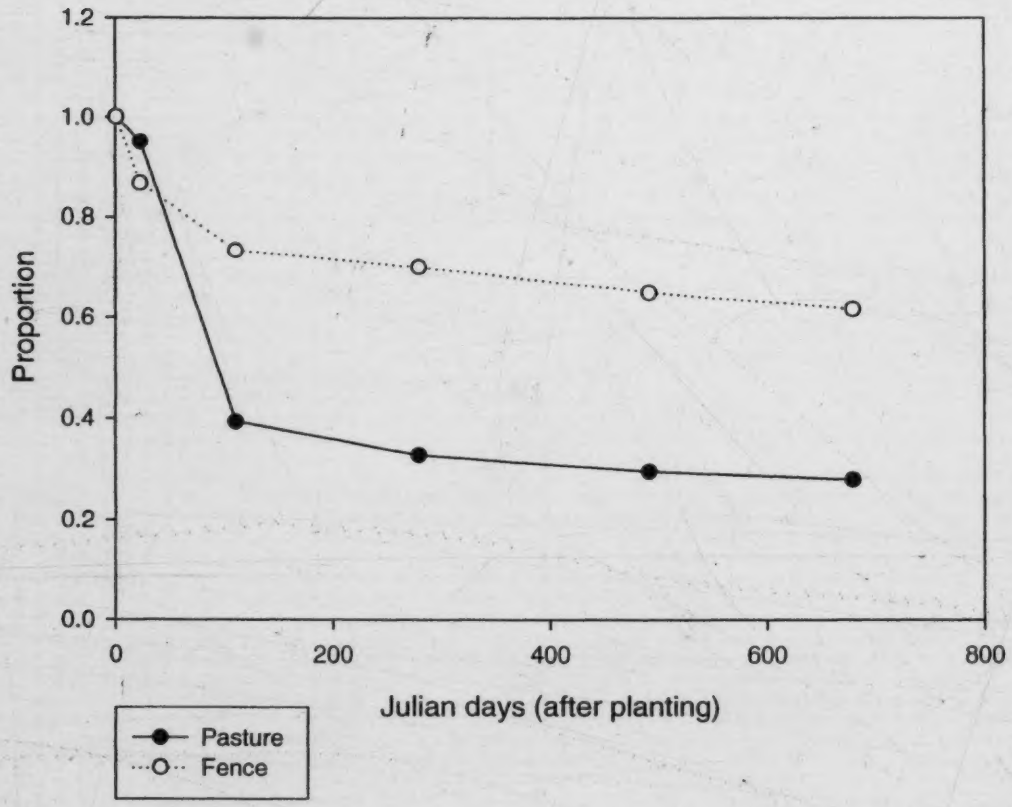


Figure 7.4 Seedling survival of each of four native tree species planted in either open-pasture or a living fence after 2 years of growth in Panama, 2004-2006. Significant differences between planting positions (open-pasture, living fence) are indicated for each category.

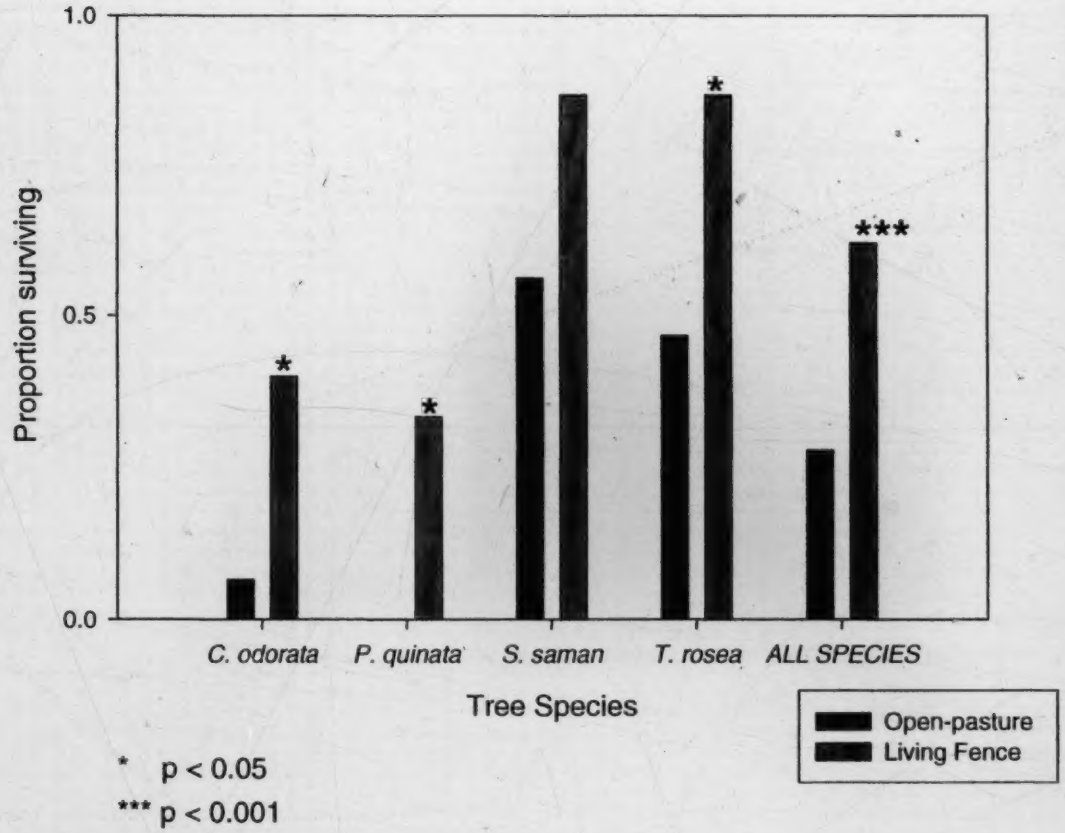


Figure 7.5 Proportion of seedlings exhibiting acceptable growth for timber production for each of four native tree species planted in either open-pasture or a living fence after 2 years of growth in Panama, 2004-2006. Significant differences between planting positions (open-pasture, living fence) are indicated for each category.

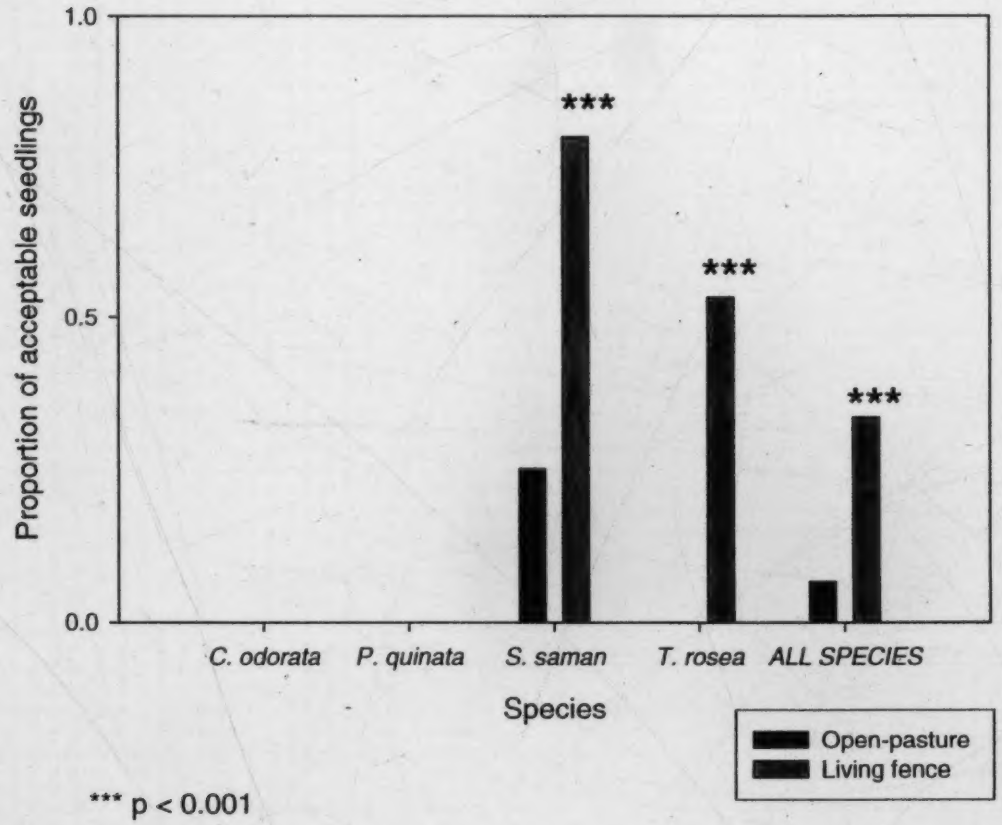
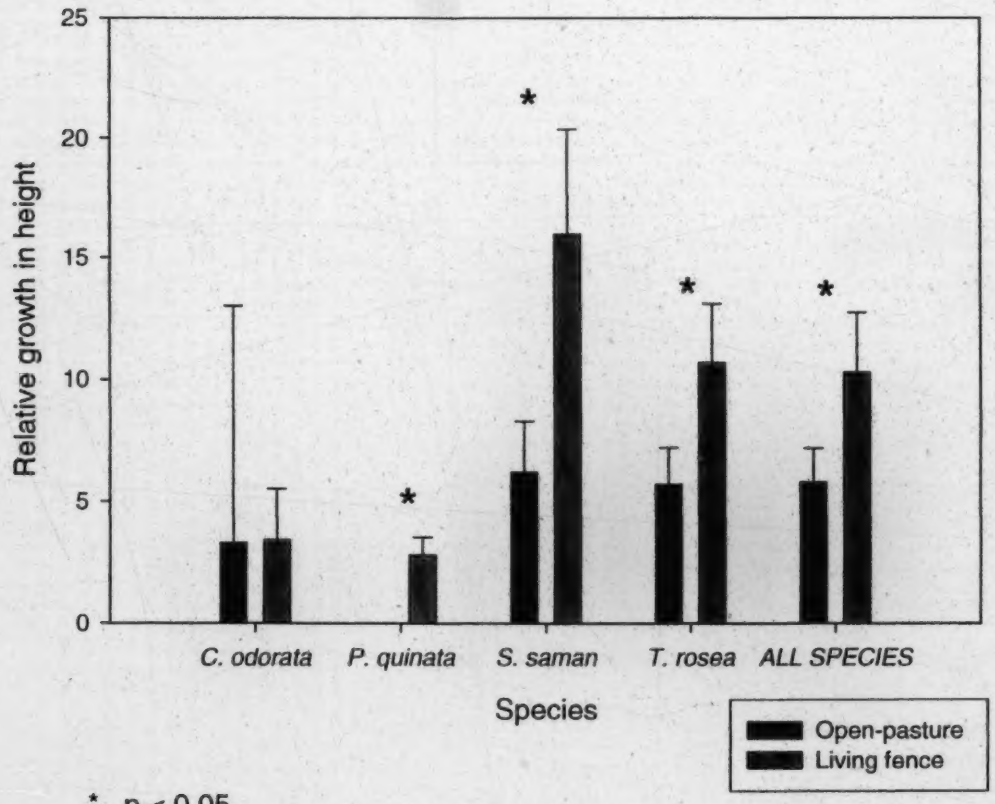


Figure 7.6 Means ± 95% confidence interval for relative height growth of seedlings after 2 years for each of four native tree species planted within either a living fence or open-pasture in Panama, 2004-2006. With the exception of the "All species" category, means are least-squared means.



7.7 Tables

Table 7.1 Mean (± 95% confidence interval) characteristics of the nearest living stakes adjacent to planted tree seedlings within living fences.

Living Stake Species	Average distance to seedling (cm)	Average basal area (cm^2)	Average height (cm)
Spondias mombin	109 ± 23	61 ± 6	355 ± 17
Jatropha curcans	102 ± 21	32 ± 4	248 ± 15
All species	106 ± 15	48 ± 4	306 ± 15

Table 7.2 Seedling survival and means (± 95% confidence interval) for seedling final height and final basal diameter after 2 years of growth for each of four native tree species established in either a living fence, open-pasture, or a monoculture plantation. Means are least-squared means except for means in the "All species" and "Plantation" categories, which are unadjusted means.

Planting environments and tree species	Survival (%)	Mean final height (cm)	Mean final basal diameter (cm)
Living fence			
C. odorata	40	72 ± 15 b[@]	3.1 ± 0.7 ab
P. quinata	33	44 ± 10 c	1.2 ± 0.2 b
S. saman	87	297 ± 83 a	4.6 ± 1.4 a
T. rosea	87	196 ± 41 ab	4.0 ± 0.8 a
Open-pasture			
C. odorata	7	66 ± 174 a	3.8 ± 3.5 a
P. quinata	na	na	na
S. saman	56	121 ± 52 a	2.9 ± 1.2 a
T. rosea	47	98 ± 23 a	2.9 ± 0.8 a
All species			
Living fence	62	191 ± 45 A[#]	3.8 ± 0.7 A
Open-pasture	28	108 ± 18 B	2.9 ± 0.8 A
Plantation			
C. odorata	50	310 ± 41[$]	7 ± 0.7
P. quinata	75	294 ± 26	7.6 ± 0.7
S. saman	93	286 ± 26	5.5 ± 0.4
T. rosea	93	487 ± 145	7.6 ± 0.4
All Species	78	352 ± 46	6.9 ± 0.3

[@] Within a column and planting environment category, means with different lower case letters differ ($p < 0.05$).

[#] Within a column, grand means (All species category) with different uppercase letters differ ($p < 0.05$).

[$] No statistical tests were applied to the plantation data as they were not part of the experimental design.

8.0 General conclusions and contributions to knowledge

Conservation, characterization, and evaluation of plant genetic resources is an international priority (FAO, 2001a). Agroforestry systems are very diverse and rely on the complimentary use of tree and annual crop genetic resources (Nair et al., 1991). Rice and maize are Panama's staple crops but their genetic diversity has not been well characterized. Upland rice, which is often farmed by swidden agriculturalists, is particularly important in Latin America (Trouche, 2005) but has not been intensively studied. Farmers' preferences for specific crop traits contributes to the farming of diversity (Bellon, 1996). Development of crop ideotypes for resource-poor farmers based on these preferences (Ceccarelli et al., 2001) has largely been limited to focus group evaluation of plant breeding program materials (Sperling et al., 2001). Native tree species diversity has been characterized in Panama (Aguilar and Condit, 2001; Condit et al., 2002) but there has been little work conducted on evaluating their performance (Condit et al., 1993).

This study focused on the characterization and evaluation of plant genetic resources that are common components of agroforestry systems in Panama. The characterization component examined maize and upland rice while the evaluation component studied the performance of native timber species. The specific objectives of these different components were:

Characterization of maize and upland rice

1. To collect and characterize the genetic diversity of maize and upland rice, farmed by subsistence farmers in Panama.

2. To provide baseline information on diversity and phenotypes and their relationship to farmers' classifications.
3. To implement a simple field survey method for identifying crop traits of importance to subsistence farmers.
4. To empirically assess the importance of maize and upland rice traits and compare and contrast these traits with formal breeding programs' objectives.

Evaluation of native timber species performance

1. To assess the initial performance (survival and growth) under plantation management of four native timber species using both on-station and on-farm trials.
2. To describe some of the practical aspects of on-farm trial implementation.
3. To evaluate the potential of a living fence to serve as a protective barrier during tree establishment in an actively grazed pasture.

Implementation of research and experiments to accomplish the above objectives led to a number of findings.

8.1 Research findings

8.1.1 Characterization of maize and upland rice

- Subsistence farmers in the Azuero region of Panama retain a significant amount of maize and upland rice diversity, with both "traditional" and "modern" crop populations being represented.

- Heterogeneity in upland rice populations grown by subsistence farmers in the Azuero region of Panama is common and often recognized as being the result of inadvertent admixture.
- Crop populations considered to be "traditional" or "modern" differed phenotypically for a number of crop traits, many of which have a history of being modified by formal breeding programs.
- The common names farmers give their maize and upland rice populations correspond to underlying genetic diversity but this association is stronger for rice than for maize.
- Simple field survey techniques can help identify crop traits of interest to subsistence farmers and may be used to construct crop ideotypes.
- Plant breeding programs appear to be studying most of the individual crop traits of interest to subsistence farmers but it is unclear if they are packaging these individual traits into desirable ideotypes.
- Farmers may have difficulty placing importance on crop traits they are not familiar with.
- A number of crop traits (yield, easy shelling/threshing, lodging resistance, earliness, pest and rot resistance, tolerance to drought and infertile soils, and fertilizer responsiveness) were important for subsistence farmers for both maize and upland rice.

8.1.2 Performance of native timber species

- On-station trials resulted in greater survival and growth estimates than the on-farm trials.

- *C. odorata* grew slower than the other native timber species.
- Plot topographic slope was negatively correlated with survival and growth metrics in the on-farm trial.
- Practical aspects of on-farm trial implementation for native-timber species paralleled that of on-farm trials for other agricultural crops.
- Seedling survival, height growth, and tree conformation in an actively grazed pasture was greater in a living fence than in open-pasture.
- Palatable tree species (i.e. *P. quinata*) did not perform well in the living fence environment due to cattle browsing.

8.3 Contributions to knowledge

This thesis contributes reviews of agrobiodiversity and on-farm survey techniques that can be used as resources by practioners in these fields. The research provides previously unavailable information on the phenotypes of maize and upland rice populations and the molecular diversity of maize farmed by subsistence farmers in Panama. Furthermore, associations between farmer classifications and genetic diversity were empirically verified and the magnitude and causes of heterogeneity in upland rice populations were described. Anecdotal reporting of associations and heterogeneity has rarely been quantified. Quantifying these associations is important if farmer classifications are to be used for guiding collection and conservation activities. Upland rice in Central America is not well studied so basic contributions such as the above are needed.

The research identified crop traits of importance to subsistence farmers in Panama and defined maize and upland rice ideotypes of potential general important in the humid tropics. We found plant breeders are researching crop traits of interest to subsistence farmers, which contrasts with past reviews that emphasize discord between the objectives of plant breeders and farmers.

Our study of native timber species under plantation management quantified differences in growth and survival for a suite of species that to date has not been experimentally compared, despite their importance for timber production in the New World. We found on-farm trials yielded lower estimates than on-station trials, an effect, which has not been well documented for tree crops. Our work presents a number of practical design and execution lessons for on-farm trials that have generally been lacking in the agroforestry literature.

We demonstrated the potential of living fences to provide protection to tree seedling establishing in an actively grazed pasture. Farmers have long accepted and established living fences along field borders. To date, no study has examined their potential as a nurse crop for establishing timber species. Such a new agronomic practice could increase tree diversity in agricultural landscapes while diversifying agricultural production. Overall this thesis research contributed to basic knowledge about the diversity of crop genetic resources in Panama and the performance of and establishment of native timber species genetic resources in agricultural landscapes.

8.3 Recommendations for future research

Research is an ongoing iterative process and studying questions related to one set of objectives leads both to new objectives and questions. New questions and objectives have evolved out of the two components of this thesis research.

8.3.1 Characterization of maize and upland rice diversity

- Can the collection and characterization of farmers' crop populations be linked with in-situ conservation activities (e.g. such as increasing germplasm availability to farmers)?
- How can information about the traits of farmers' crop populations be combined with information about farmers' preferences for specific traits in order to implement a breeding program that effectively uses available germplasm to produce varieties with desired traits?
- Can the relative importance of traits be rigorously assessed empirically by using different field survey techniques?

8.3.2 Initial performance of native timber species

- How do differences in farmers' agronomic practices (e.g. weeding, fertilization) affect initial tree seedling performance?
- How do specific soil properties (e.g. chemical, physical) affect the initial performance of tree species?
- How does competition with living fence stakes affect the performance of tree species planted into a living fence?

- What suite of tree species is best suited to performance in living fences under a wide range of living fence (e.g. species composition, density) and pasture (e.g. stocking density, pasture composition) conditions?

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10.0 Appendices

Appendix 3.1 Glossary of technical terms used in on-farm survey based studies

Technical terms	Explanation
Buffer questions	Relatively neutral questions preceding sensitive questions
Sampling unit	The object of interest to be sampled by a survey.
Sampling universe	The population that consists of all the objects of interest to a survey.
Sampling frame	Databases of objects of interest to the survey that correspond to the population of interest.
Probing	Interviewing technique in which the interviewer inquires more deeply about specific topics
Telescoping	The placement of events before or after their actual occurrence in time.
Recommendation domain	Groupings of farmers that are felt to be rather uniform with respect to their acceptance of agricultural practices and/or technologies.
Cluster sampling	Sampling that defines where objects of interest occur and then samples these locations or entities to obtain a sample of objects.
Focus groups	Interviews conducted with multiple participants that allow and encourage participant interaction.
Questionnaire	An interview that is written down and has a highly specific form in terms of question wording and order.
Panel survey	Surveys that track a group of participants through time.
Stratification	Grouping objects of interest based on specific attributes. Usually applied prior to sampling.
Context effect	When a preceding question alters the response to a subsequent question
Pair-wise ranking	Ranking of all pairs of items one at a time
Interview context	The physical and social setting in which an interview is administered.

Appendix 4.1 PCR master mix recipes for the amplification of different microsatellite marker in bulked maize DNA samples.

Marker Name	Primer (ul)	Buffer (ul)	NTPs (ul)	MgCl (ul)	Taq (ul)	Water (ul)	DNA (ul)	PCR program
phi063	1.0	1.0	1.2	0.4	0.15	4.75	1.5	Q64
phi065	2.0	1.0	1.2	0.4	0.15	3.75	1.5	Q56
phi079	1.0	1.0	1.2	0.4	0.15	4.75	1.5	SSR62
phi102228	1.0	1.0	1.2	0.4	0.15	4.75	1.5	SSR54
phi299852	1.0	1.0	1.2	0.4	0.15	4.75	1.5	Q60
umc1161	1.5	1.0	1.2	0.4	0.15	4.25	1.5	SSR56
umc1196	0.6	1.0	1.2	0.4	0.15	5.15	1.5	SSR58
umc1447	0.8	1.0	1.2	0.4	0.15	4.95	1.5	Q60
umc1545	1.0	1.0	1.2	0.4	0.15	4.75	1.5	Q60
umc1917	1.0	1.0	1.2	0.4	0.15	4.75	1.5	SSR52
umc2250	1.5	1.0	1.2	0.4	0.15	4.75	1.5	Q58

Appendix 4.2 PCR reaction programs for microsatellites amplified in bulk DNA samples of maize populations collected in Panama.

Program	Step	Temp(°C)	Time (min)	Instructions
SSR52	1	94	2	
	2	94	1	
	3	52	2	
	4	72	2	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End
SSR54	1	94	2	
	2	94	1	
	3	54	2	
	4	72	2	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End
SSR56	1	94	2	
	2	94	0:30	
	3	56	1	
	4	72	1	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End
SSR58	1	94	2	
	2	94	1	
	3	58	2	
	4	72	2	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	forever	
	8			End
SSR62	1	94	2	
	2	94	0:30	
	3	62	1	
	4	72	1	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End

Program	Step	Temp(°C)	Time (min)	Instructions
Q56	1	94	2	
	2	94	0:30	
	3	56	1	
	4	72	1	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End
Q58	1	94	2	
	2	94	0:30	
	3	58	1	
	4	72	1	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End
Q60	1	94	2	
	2	94	0:30	
	3	60	1	
	4	72	1	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End
Q64	1	94	2	
	2	94	0:30	
	3	64	1	
	4	72	1	
	5			Repeat steps 2-4, 29 times
	6	72	5	
	7	10	Forever	
	8			End

Appendix 4.3 The size and average frequency of alleles detected in Panamanian maize populations by different microsatellite markers.

Marker	Allele size in base pairs	Average Frequency	Marker	Allele size in base pairs	Average Frequency
phi063	161	0.03	umc1196	130	0.16
phi063	170	0.70	umc1196	135	0.04
phi063	174	0.27	umc1196	140	0.14
phi063	178	0.01	umc1196	144	0.51
phi065	127	0.73	umc1196	149	0.03
phi065	138	0.16	umc1196	151	0.02
phi065	143	0.11	umc1196	156	0.09
phi079	177	0.20	umc1447	110	0.17
phi079	182	0.05	umc1447	113	0.01
phi079	185	0.35	umc1447	115	0.25
phi079	187	0.27	umc1447	119	0.56
phi079	192	0.13	umc1447	122	0.01
phi102228	120	0.83	umc1545	65	0.16
phi102228	125	0.17	umc1545	73	0.03
phi299852	106	0.00	umc1545	76	0.76
phi299852	107	0.16	umc1545	77	0.01
phi299852	110	0.32	umc1545	79	0.05
phi299852	112	0.05	umc1917	122	0.01
phi299852	117	0.08	umc1917	128	0.57
phi299852	119	0.33	umc1917	130	0.00
phi299852	125	0.01	umc1917	134	0.13
phi299852	132	0.01	umc1917	137	0.15
phi299852	135	0.02	umc1917	140	0.01
phi299852	138	0.03	umc1917	143	0.13
umc1161	130	0.01	umc2250	133	0.20
umc1161	135	0.03	umc2250	139	0.00
umc1161	142	0.76	umc2250	149	0.79
umc1161	145	0.03			
umc1161	148	0.17			

Appendix 5.1 Informed consent document used to outline farmers' rights

CONSENT FORM

My university requires that I formally ask your permission to talk with you. It is important that you agree:

1) **That you understand this work is for university schoolwork.**
2) **That I have presented my project to you.**
3) **That you have had a chance to ask questions.**
4) **That you understand that I will be taking notes.**
5) **That you can choose not to participate at any time.**
6) **That you understand that your privacy is protected.**
7) **That you understand aggregate data may be published in journals.**
8) **That there is no compensation for participation but I will pay the cost of any seed you can provide me with.**
9) **That seed collection may involve removal of seed from your field if you want.**
10) **That I do not believe that you are at risk.**
11) **That you can contact supervisor, my Francisco Santamaria, or me if you have future questions or concerns.**
12) **That the seeds are for research and any further use or distribution will require your permission.**

Do you consent to participate? Yes / No

Researcher's Signature_____

Brian Love

Graduate Student
Department Agricultural, Food and Nutritional Science
University of Alberta
769 General Services Building
Edmonton, Alberta T6G 2H1
Canada
brianl@ualberta.ca
780-492-8517

Dean Spaner
Assistant Professor
Department Agricultural, Food and Nutritional Science
University of Alberta
4-16D Agriculture and Forestry Centre
Edmonton, Alberta T6G 2H1
Canada
dean.spanner@ualberta.ca
780-492-2328

Francisco Santamaria

Cuerpo de Paz
Apartado 55-2205
Paitilla, Cuidad de Panama
Panama
269-2100

Appendix 5.2 Interview format used to obtain data on maize and upland rice traits of importance to subsistence farmers in Panama.

FECHA:_____ **CODIGO DEL PRODUCTOR** _____

Nombre:	
Edad **(Años cumplidos)**	
Sexo: **(1=Masculino, 2=Femenino)**	
Educación **(Años de escolaridad terminada)**	
Sabe leer y escribir **(1=Si 2=No)**	
Uso de la tierra **(1=Rastrojo de Monte, 2=Rastrojo de cultivos)**	
De la comunidad o inmigrante **(1=Comunidad, 2=Inmigrante, 3=Otro epecifique)**	
Ud. trabaja: 1=Tierra propia 2=Tierra familiar 3=Tierra arrendada 4=A media	
¿Hace cuánto tiempo llegó a la comunidad? **(en caso de inmigrante)**	

ARROZ

Nombre	Lo bueno	Lo malo

MAIZ

Nombre	Lo bueno	Lo malo

CARACTERISTICAS PARA NUEVAS VARIEDADES

Maíz:	**Arroz:**